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PHENOLOGY, NATURAL HISTORY AND SPECIES DIVERSITY OF WEB-BUILDING SPIDERS ON THREE TRANSECTS AT WAU, NEW GUINEA

By **Michael H. Robinson, Y. D. Lubin** and **Barbara Robinson**[1]

Contents

Abstract: Phenology, species composition and diversity of web-building spiders were studied in a relatively nonseasonal, tropical montane area. Weekly censuses were made during the period of May 1970 to May 1971 of all web-building spiders along three 100-metre transects in the vicinity of Wau, New Guinea. The physiognomy of the transects, and the natural history and distribution of the spider species encountered are detailed.

The year was divided, somewhat arbitrarily, into a six month dry and six month wet season. Seasonal distributions of spiders were analyzed in several ways to determine the overall trends. Distribution patterns of each species and of populations on each transect are compared and discussed. Though seasonal variations are less pronounced than in temperate regions, some species show distinct dry or wet season population peaks of adults

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and/or immatures.

Species diversity is discussed in the light of theories of structural complexity of the habitat, competition between species, and climatic stability. We suggest that biological accommodation resulting from sustained coexistence of species in tropical areas may lead to high species diversity.

INTRODUCTION

Turnbull (1973), in a comprehensive review of studies on the ecology of spiders that lists 331 references, remarks that there have been "a wide variety of community analyses of spiders from a wide variety of environments" (ibid, p. 322). This statement is only true if the qualification "non-tropical" is added to the statement about a wide variety of environments. A basically similar statement could be made about phenological studies of spiders. In the last ten or so years there have been a number of detailed phenological studies of considerable depth (see references, for instance, in Merrett 1967, 1968, 1969 and Russell-Smith & Swann 1972). Again, however, most of these were carried out in the North Temperature regions, particularly those of Europe.

Absence of ecological studies of tropical spiders reflects the distribution of biologists rather than that of the spiders themselves. In fact, quantitative studies of tropical arthropods, in general, are mostly very recent (see Elton 1973). All this is highly regrettable since most tropical faunas are rich in both numbers and species of spiders. In addition, there is, at the moment, little agreement among tropical biologists on whether conditions in various parts of the tropics differ in stability or predictability from conditions in temperate regions (see Discussion). At least a major part of this question can only be answered by phenological studies. We here report the results of the weekly censusing of web-building spiders carried out at three sites at Wau, Morobe District, New Guinea over the period May 1970 to May 1971. The study was carried out to determine what fluctuations occurred in the numbers, age and species composition, and species diversity of spider populations living in an area that had a rich spider fauna ***and*** a relatively benign climatic regime[2]. The study yielded data on natural history, phenology, and, to a lesser extent, species diversity. Although these categories are by no means exclusive, we use them herein as a descriptive convenience.

THE METHOD OF CENSUSING

Our censusing technique was simple and non-destructive. For most of the weekly censuses two of us (M.H.R. and Y.D.L.) acted as observers and the third (B.C.R.) acted as recorder. The observers walked along the edge (100 metres) of each transect, carefully inspecting the vegetation within two metres of the edge and up to two metres in height (if any). The numbers and nature (sex, species, family, etc.,) of all web-building spiders were called out and recorded on standard data sheets. For convenience the hundred metre transects were marked out in subdivisions of ten metres. An important aspect of the census technique is the use of two observers which allows for the second-in-line observer to ***competitively*** check observations of the first. Since the object of the study was to produce an absolute count of essentially non-vagrant animals, the censuses

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[2] We felt, intuitively, that the climatic regime was benign compared with other tropical regions where we have worked. The results of this study suggest that this judgement was valid (see Discussion).

were not either timed or time-limited. The censuses were always conducted on the same day of the week, Sunday, starting at 2 p.m., and the total time involved (at the sites) varied between two and three hours weekly.

THE EFFICACY OF THE SAMPLING METHOD

Numerous techniques have been utilised for sampling arthropod populations. Southwood (1966) gives an excellent review and critique of many of these. Turnbull (1973: 323–326) gives a review of the techniques used to study spider populations and concludes that the three most common techniques (sweep-netting, pitfall trapping and beating) all leave a great deal to be desired "as it is, virtually all quantitative data on spider populations are at least suspect" (p. 325). Southwood (1966: 186–187) suggests that direct searching may not produce comparable data when different habitats are involved because "the efficiency of search is bound to differ" (p. 186). Turnbull (1973: 325) suggests that three factors bias the results of visual search: 1, the prevalence of cryptic forms; 2, the nonobjective searching of different habitats; 3, variations in the searching power of the observer. We believe that some, if not all, of these objections are inapplicable to counts of web-building spiders. These spiders are, to our view, probably more easy to count by simple inspection than any other terrestrial invertebrates. This is largely because webs are fairly conspicuous structures, inevitably much larger than their constructors, and because the strategy of operating webs requires that they by placed in locations through which insects pass, they are almost always in gaps between vegetation. Although some spiders may be cryptically coloured, their webs make them much easier to detect (at least to the human eye) than cryptic insects that rest on a matching substrate. A further effect of web-building is to restrict the vagility of the spider during the period when the web is in operation. The censuser of web-building spiders is not therefore confronted with the problems that confront (for instance) the bird counter (see Yapp 1956).

The objection to the technique of visual inspection based on differences in 'inspectability' between habitats can be a valid one if there are major differences between habitats in levels of illumination. Thus in tropical forests the level of illumination may be very low indeed and also vary considerably between seasons. We did not encounter difficulties in seeing webs on any of the transects because of low illumination. Differences in vegetation density between transects could affect the censusing of many organisms but such problems are largely ameliorated in the case of web-building spiders because of the tendency (see above) to operate webs in insect flight paths rather than within vegetation tangles.

On Turnbull's (ibid) third point of criticism of the technique of visual searching — the fact that the searching power of the observer varies in time — we feel that this had little effect on the consistency of the census. We used two searchers working competitively and broke up the searching period with 'rests' when we moved between transects. In addition, since we always censused the transects in the same order, any errors due to eye-fatigue should be distributed in a consistent manner.

It is important to add that the census was of diurnal web builders and that the fairly extensive fauna of nocturnal web builders is largely excluded from our samples. These spiders either take their webs down at dawn or leave them in situ only if the night's catch was insufficient.

We feel that our censusing technique measured real differences between spider populations of the three transects as well as real phenological differences, and we think that, for the types of spiders involved, it is more reliable than any other method. It does not involve removing individuals from a population nor damaging the habitat in any way.

Two further possible sources of error may not be immediately obvious to the non-arachnologist. Firstly, it is possible for araneids to be present without building webs. Some spidres stop web-renewal several days before egg-laying (Robinson & Robinson 1973). However, this is not likely to be a major source of error since many species remain in skeleton webs until the actual day of laying. Spiders that have very fragile webs may have these destroyed by strong winds, or rain, or both, and census results could be affected by the weather immediately prior to the census period. Our general observations show that such spiders (*Tetragnatha* species in particular seem to have very fragile webs) rebuild very soon after rainfall has ceased. We never carried out censuses during rains. A remaining possible source of error is that several days of adverse weather could affect a large section of the web-building population adversely. We have no evidence of such an effect on our censuses.

IDENTIFICATION OF THE SPECIES

At the beginning of the study period we identified araneids to genera and recognised, but did not name, the species within the genera. Accordingly we assigned initials to each species and recorded them in this manner. Later Father Chrysanthus was able to identify all but the new species. These are still listed in the accompanying tables and graphs with our original designation. We have not assigned *Argiope* males to species, even when these were found in the webs of females, since males of this genus appear

Table 1. Known geographical range for species found on transects (from Bonnet 1955, 1956, 1957, 1958).

Species	Range
Cyclosa insulana	Europe, N. Africa, India, Burma, Malaysia, Japan, China.
Cyclosa bifida	Burma, Malaysia, Tonkin.
Gasteracantha theisi	Indo-China, Malaysia, Polynesia, Australia.
G. taeniata	India, Burma, Malaysia, Polynesia, Australia.
Argiope aemula	India, Burma, Thailand, Indo-China, New Guinea, Australia.
A. picta	Indonesia, New Guinea, Solomon Is., N. Hebrides, New Caledonia, Australia.
A. reinwardti	Malaysia, Sumatra, Djawa, Philippines, New Guinea, Australia.
Nephila maculata	Africa, Malagasy, Sri Lanka, Thailand, Burma, India, Indonesia, Borneo, China, Japan.
Araneus theisi	Polynesia, S. Africa, Congo, E. Africa, W. Africa, Egypt, U.S.A., Sumatra, Djawa, New Guinea, Japan, Australia, Malaysia.
A. laglaizei	India, Himalayas, Sri Lanka, Burma, Thailand, Malaysia.
Poltys illepidus	Australia, Malaysia.
Leucauge papuana	Malaysia, New Guinea.
L. grata	Malaysia, New Guinea, Polynesia.
Psechrus argentatus	Sri Lanka, China, Malacca, Sulawesi, Malaysia, Bismarck Archipelago, Amboina.

Note. We have substituted modern names for those used in Bonnet where these are reasonably equivalent. In all other cases we have used a direct translation from the French.

in the webs of the 'wrong' species. Neither have we assigned immatures of ***Argiope***, ***Araneus***, ***Gasteracantha*** and ***Cyclosa*** to species, since early stages, up to third or fourth instar, are extremely difficult to determine without handling. Theridiids, uloborids, pholcids, tetragnathids, psechrids and linyphiids are assigned to the lowest taxon for which we could get an identification (some of these groups are very poorly known from New Guinea).

Chrysanthus (1958, 1959, 1960, 1961, 1971) gives descriptions and some general notes on many of the araneids that we encountered during the censuses. Table 1 gives the known geographical range of those species for which there are good data.

THE TRANSECTS

The descriptions of the three transects that appear below are based on field notes that recorded estimates and not measurements, and we made no attempt to analyze the floristic nature of the vegetation cover or to *measure* its structural diversity.

Transect I (see Fig. 1) bordered the north side of a trail through the woodland[3] on the boundary of the Wau Ecology Institute arboretum. For 70 metres of its length it was shaded by overhanging trees, and bordered by shrubs and trees for at least 60 metres of its length. At the eastern end of the transect the trail emerged from the woodland and there was a transition zone marked by an increasing proportion of grassland herbs and forbs interspersed by small bushes. No rocky outcrops occurred on this transect and the ground was flat over the greatest part of its length.

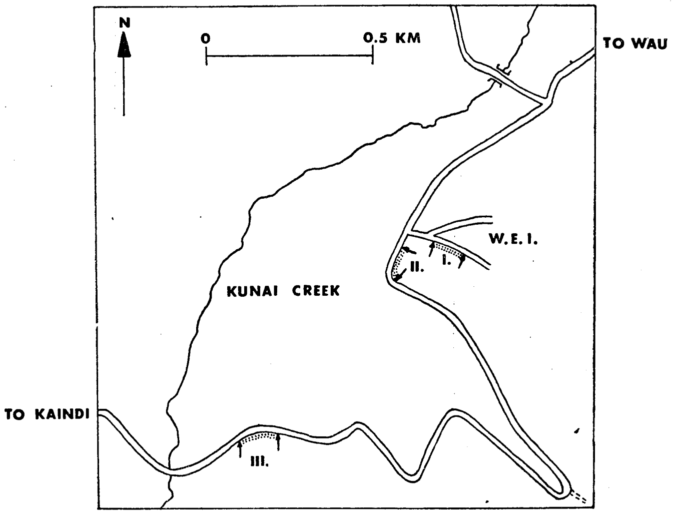

Fig. 1. Map of the Wau valley, New Guinea, showing the locations of transects I, II, and III.

Transect II was situated on the southern edge of the Wau-Mount Kaindi road about 200 metres north of Transect I, at the nearest point, and at roughly the same

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[3] A former coffee plantation now with many tall trees forming a partial canopy (for a listing of some of the tree species see Robinson & Robinson 1973a).

altitude (1150 metres). It lay entirely outside the woodland from which it was separated by a hedge of vines, ***Hibiscus*** and thorny shrubs. The hedge was included in the transect at several places. The extensive roadside-verge vegetation, consisting of grasses and herbs, was not cut during the census year. Incidences of damage to subsections of transects, by heavy rains, flooding or partial cutting, are detailed in Table 2. For the first 50 metres the verge was flat and usually more than two metres wide, so that the only woody plants included in this zone were represented by overhanging branches from the hedgerow. In the upper 50 metres, the verge became a steep, and, in places, a rocky bank. In general, this transect was very exposed and well-lit and was only shaded at the hedgeside. Transect I was roughly east/west in orientation and transect II ran, for the most part, northeast/southwest.

Table 2. Disturbances of the transects during the census period.

Date	Transect I	Transect II	Transect III
Jan. 8	———	Vegetation flattened by heavy rains	———
Jan. 17	Grass cut, 1–30 m.	———	———
Feb. 14	Grass cut, 1–10 m.	———	———
Feb. 20	Heavy rains damaged vegetation on all transects		
Apr. 4	Grass cut, 1–10 m.		
Apr. 25	Grass cut, 1–20 m.		Grass cutting
	Heavy rains throughout April resulted in considerable damage to vegetation		
June 7	Tree fall flattened vegetation, 30–40 m.	———	———
June 14		———	Heavy rains, no census
Jul. 19	Vegetation damaged, 30–60 m	———	———
Jul. 26	Vegetation damaged, 1–10 m & 20–30 m	———	———
Aug. 2	Grass cut, 1–80 m	———	———
Sept. 3	Grass cut, 1–70 m	———	———
Oct. 3	Grass cut, 1–70 m	Grass cut, 1–30 m	———
Oct. 25	121.9 mm of rain fell between Oct. 22 and 25 resulting in some vegetation damage on all transects		
Nov. 15	Grass cut, 1–70 m	———	———
Nov. 28	Heavy rain on Nov. 27 resulted in vegetation damage on all transects		
Dec. 6	———	Grass trimmed	———

Transect III was situated about 2 miles (by road) from transects I & II on the edge of the Wau to Mount Kaindi road, close to Kunai Creek. At 1370 metres altitude, it bordered montane forest, curved markedly along its length on an east/west line and faced mainly north. Unlike the other two transects, transect III contained little flat ground, consisting mainly of strongly sloping mountainside. It also sloped considerably along its length. For the upper 40 metres creviced rocky outcrops predominated at the foot of tall trees. In this region, ferns were well represented in the herb layer. In the lower portions of the transect, rocky outcrops were infrequent, tall trees less densely packed and a good topsoil was present. This region supported a more luxuriant herb layer in which bramble-like plants were often abundant. The area was sheltered and generally wet.

Subjectively we would rank the transects, in regard to shade, exposure, vegetational and physical complexity (the latter term describing relief and presence of rocky outcrops), as follows: transect I the most shade, transect II the least; transect II the most exposed, transect I the least. Transect I had the most complex vegetational structure and the most simple physical structure. Transect III was physically the most complex and had the second most complex vegetational structure. Transect II had the simplest phytophysiognomy. From this ranking we would expect that climatic extremes would be greatest in transect II. In terms of source areas for immigration of spiders or spiderlings, transect I was inside a wooded area of several acres with a rich invertebrate fauna. Transect II was on the outside margin of this and its boundary hedge could possibly constitute a minor barrier; it faced an extensive coffee plantation that was intensively cultivated. Transect III was on the lower margin of an extensive area of mature, mostly undisturbed, montane forest. The forest below the road (and the transect) had been heavily cut along most of the length of the transect.

Since a detailed vegetational analysis of the transects was beyond our competence, we attempted to classify the transects in terms of availability of web supports for spiders with different web building strategies. This assessment produced seven categories of potential web sites. Table 3 ranks the transects on a scale of 0–10 for each of these categories. The ranking is based on an examination of each of the ten subdivisions of the transects. Web site availability in these was scored for presence or absence on each subdivision and not for numbers within such sections since this would have presented major problems in designation. Thus a score of 7, for example, for sites for large aerial webs means that this type of web site was present on seven sections out of ten. Table 3 also scores the web sites for the three transects on a present or absent basis. Thus, if a web site class was present on five or more sections, it is scored as present and those with scores of less than five are classified as absent.

Table 3. The availability of potential web sites, scored for presence in each 10-m subtransect, and for presence or absence on each transect. (See text).

Web sites Transects	I	II	III	I	II	III
For large aerial webs	7	2	2	+	–	–
For small aerial webs	9	5	6	+	+	+
For large webs within herb layer	4	9	5	–	+	+
For small webs within herb layer	8	10	10	+	+	+
For horizontal webs within herb layer	10	8	8	+	+	+
For funnel webs	2	5	9	–	+	+
For webs built in crevices	0	0	7	–	–	+
Total	40	39	47	4	5	6

THE NEW GUINEA FAUNA

New Guinea, the second largest island in the world, has a rich and diverse fauna which can be regarded as continental rather than limited and insular. Although there are no studies of the zoogeography of spiders relating to this region, there is a considerable number of treatments of the zoogeography of insect groups occuring in New Guinea. Gressitt (1961) contains an extensive bibliography. He notes (1961: 42) that "…the insect distribution picture is different from that of the vertebrate animals." The insect fauna is primarily Oriental, while the mammals, birds and reptiles have many affinities with those of Australia. A recent discussion of the geological and geographical history of New Guinea is to be found in Darlington (1965).

RESULTS

NATURAL HISTORY OF THE SPIDERS

The distribution of species between transects, and within transects with time, allow certain inferences to be made about habitat preferences and other aspects of natural history. These are detailed in the species-by-species account below, and in Fig. 2, 3, and 4.

ARANEIDAE

Nephila maculata (Fabricius)

All the evidence suggests that this large spider is a woodland species requiring the existence of woody vegetation as supports for its large, strong web (see Robinson & Robinson 1973 for details of web dimensions). Adult females were present on transect I on 30 out of 52 weekly censuses and immatures were absent on only four occasions. In the nearby Arboretum the adults were present all the year round and egg-laying occurred in all months of the year (Robinson & Robinson 1973). On the more exposed transect II, adult females were present on only 18 occasions and at transect III were never recorded. On transect III, immatures were present all the year round, presumably 'seeded' from the nearby forest. It seems probable that the absence of adult females from this site can be correlated with the absence of web sites. Adult males were recorded from transect III. These occurred in the webs of immature females.

Argiope aemula (Walckenaer)

This, the largest of the Wau *Argiope* species, seems to be the ecological equivalent of *Argiope argentata* (Fabricius) in that it is an open-area species. It occurred with maximum frequency on transect II where adult females were present on over 90% of censuses. It was present on transect I on 48% of the censuses and on transect III on only 26% of the censuses. This view is confirmed by our other studies in the Wau area. The species builds a cruciform stabilimentum, when the structure is present in a 'perfect' form, and this does not cross the hub region. (See Robinson & Robinson, in press, for details of the stabilimentum building in this species and *A. picta* and *A. reinwardti*).

Argiope picta L. Koch

This large species seems to prefer more shaded areas and can be described as a forest-fringe species that builds its webs in low bushes and tall herbs. It occurred throughout the year on transect I, on over 96% of censuses on transect II, and was only observed once on transect III. When present, the 'perfect' stabilimentum is cruciform.

Argiope reinwardti (Doleschall)

This species is encountered most frequently in shaded woodland locations and often exploits rock faces as web sites. It was the dominant *Argiope* species on transect III where it was present throughout the year. It occurred on transect I on over 63% of the censuses and on the more exposed transect II on 48% of censuses. The 'perfect' stabilimentum is dense, cruciform, and crosses the hub. On webs built against rock faces, the

Fig. 2. Presence of spider species on transect I during the census period.

spider frequently rests on the side facing the rock, behind the stabilimentum.

Argiope species F

This, the smallest *Argiope* species that we have seen, was first discovered on transect II living in tall grass. We subsequently found it in the eastern grassy section of I, but

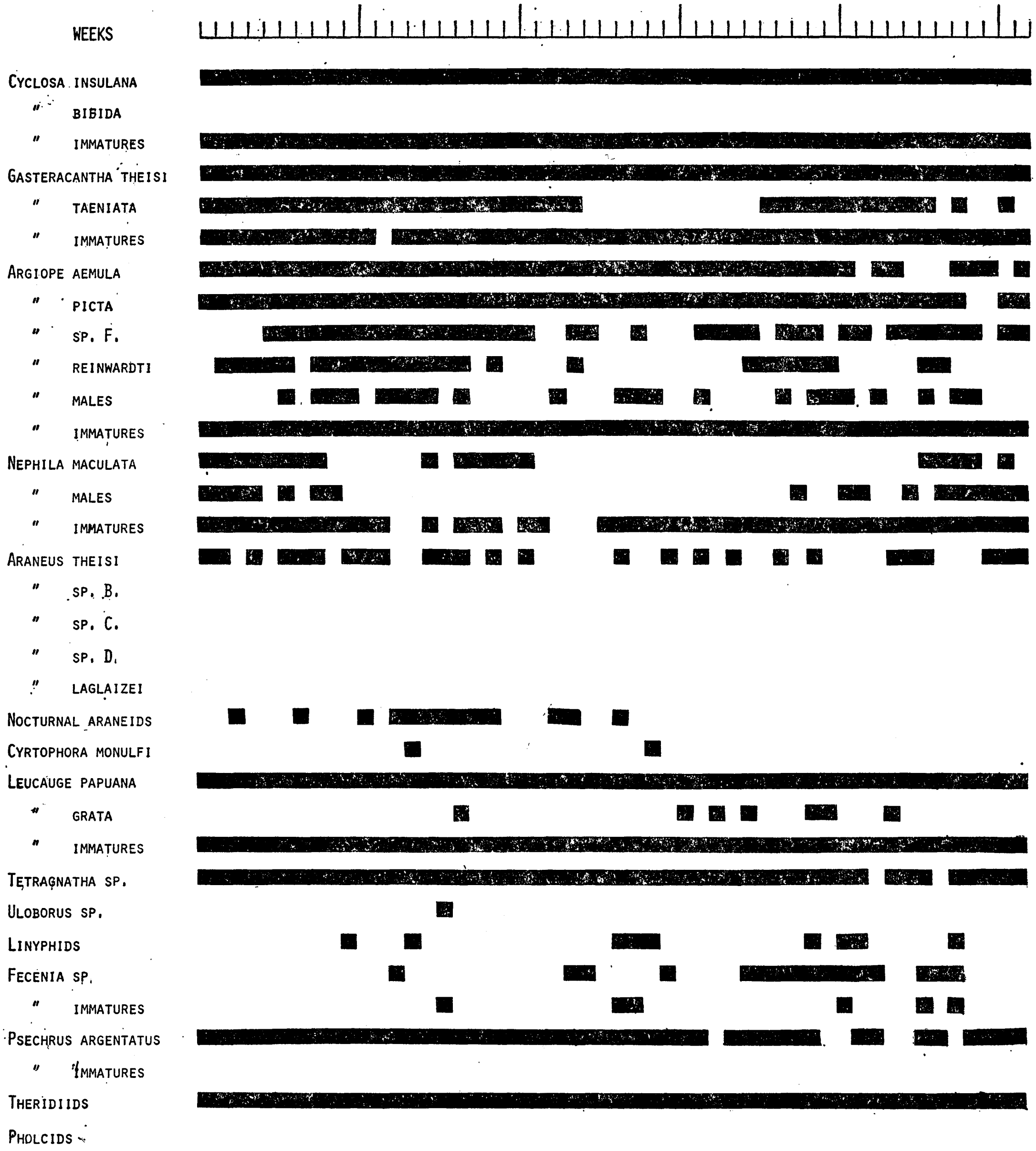

Fig. 3. Presence of spider species on transect II during the census period.

never recorded it from transect III. It occurred quite frequently on transect II (71% of occasions) but we never recorded more than eight individuals on any one occasion. It occurred on more than 44% of the censuses on transect I with a maximum of three individuals. Again, the 'perfect' stabilimentum is cruciforum, not occluding the hub.

Fig. 4. Presence of spider species on transect III during the census period.

Argiope immatures

Immature *Argiope* species were present on transect I for over 96% of the censuses and all the year round on the other two transects. Since *Argiope picta* predominated in numbers of occurrences *and* individuals on transect I, it seems reasonable to assume that most of the immatures on that transect were of *A. picta* (particularly since *A.*

aemula and *A. reinwardti* were rare or absent in the surrounding woodland). The absence of *Argiope* immatures on only 3 weeks out of 52, in transect I, suggests that reproduction was virtually all-the-year round. On transect III, *Argiope reinwardti* clearly predominated in number of occurrences *and* number of individuals, and the majority of immatures present throughout the census period were almost certainly of this species. The situation on transect II, where both *A. aemula* and *A. picta* were virtually present throughout the year (the former absent five times, and latter twice), makes it impossible to assign immatures to any one species.

Other *Argiope* species

We collected *Argiope trifasciata* Forskal from the Wau valley, on roadsides in grasslands, but it did not occur on the transects. *Argiope aetheria* (Walckenaer) was common in disturbed coastal forests near Lae but we did not record it from the Wau valley.

Gasteracantha theisi Guérin

This species builds its fine-meshed web above the herb layer and is a woodland-fringe species. It occurred all the year round on transects I & II and was rare on transect III (recorded for 7 out of 50 weeks). The species was most abundant on transect I (maximum number 45, minimum 8) and less abundant on transect II (range 21–3).

Gasteracantha taeniata (Walckenaer)

This variably coloured species — the laterally extended opisthosoma varies from white, through lemon-yellow, to deep orange — builds fine-meshed webs high above the ground in shaded locations. It was the dominant *Gasteracantha* species on transect III (84% of censuses), occurring less frequently on the other two transects and never abundantly. It may well be a near-canopy form.

Other *Gasteracantha* species

We collected two other *Gasteracantha* species from the Wau valley, *Gasteracantha* sp. A and *G. brevispina* Doleschall. Both species were absent from the transects. *G. brevispina* was very common on electric overhead power lines around the laboratory buildings of the Wau Ecology Institute. It may require web supports that are further above the ground than any included in the transects.

Cyclosa insulana (Costa)

This species is highly variable in coloration, so much so that we originally designated specimens as species A, B & C. It does not seem to be a forest or woodland species but apparently prefers clear sunny areas. Webs are usually built from tall grass or shrubs. The distribution among the three transects reflects these habitat preferences. It occurred on transect I on 54% of the censuses, on transect II all-the-year round, and on transect III on 13 out of 50 occasions. The species has a stabilimentum of ribbon silk that is highly variable in form.

Cyclosa bifida (Doleschall)

This species, a 'tailed' form, occurred only on transect III. Elsewhere in the Wau valley it occurred in mature forest, and we conclude that it is a forest species that occurred on transect III as an outcrop of the forest population.

Araneus theisi (Walckenaer)

A small species which occurred infrequently on transect I (4% of censuses) and transect III (24%). It did not occur at all on transect II. We conclude that it is a woodland species and shade-loving.

Araneus species B

This species occurred only on transect III where it was encountered frequently (78%) but never in large numbers (maximum 6). We assume that is a forest understorey species.

Araneus species C

Occurred only on transects I and III. On transect I it was infrequent (11.5%) while on transect III it occurred frequently (84%). In neither locality was it numerous (maximum 8). This spider constructed a retreat in a folded grassblade.

Araneus laglaizei (Simon)

This tailed spider somewhat resembles *Arachnura* sp. in appearance and occurred once Somewhat on transect I. It was encountered very rarely in the Wau valley.

Nocturnal Araneids

We were unable to determine the species of nocturnal araneids without disturbing the web. From web characteristics we tentatively identified many of them as ***Poltys illepidus*** C. L. Koch. This nocturnal araneid sometimes left its web *in situ* by day and was recorded for all three transects. The large web spans gaps in woody vegetation and the spider sits in a curled-leaf retreat by day and at the hub by night. We assume that it is ecologically similar to *Eriophora fuliginea* (see Robinson, Robinson & Graney 1972). Like *Eriophora* it may only leave its web *in situ* by day if the previous night has yielded few prey items. Our census records may not, therefore, reflect its true distribution.

Cyrtophora

No adult *Cyrtophora* sp. occurred on any of the transects, although a large colony of *Cyrtophora moluccensis* occurred 600 metres north of transect I and there were several colonies of this species on the Mount Kaindi road above transect III. The grass-living solitary *C. monulfi* was also common on roadside verges about half a mile southwest of transect II. Immature *Cyrtophora* were recorded on one occasion on transect I, twice on transect II, and more frequently on transect III (32%). All *Cyrtophora* webs are relatively permanent structures of much greater durability than those of other araneids and quite conspicuous. (Details of the web structure, natural history and behaviour of the *Cyrtophora* species found at Wau appear in Lubin, in press.)

TETRAGNATHIDAE

Tetragnatha sp.

An elongate *Tetragnatha* sp., building horizontal webs slightly above, or at the surface of the herb layer, was regularly present on all transects (transect I=98%, II=96%, III=94%). The species reached maximum numbers (69) on transect I. We conclude that it is a woodland fringe to woodland species, but with a capacity to exploit less favourable habitats. This species operates its webs by day. On days when the census followed morning rains, the spiders were often rebuilding their webs during the census period.

Leucauge papuana Kulczynski

This species rivals the *Tetragnatha* sp. (above) in its success on all three transects. Transect I was apparently the least favorable habitat with 92% occurrences but never more than 14 individuals. The species was present all the year round on transects II and III with maximum numbers of 46 and 35, respectively. The species builds its horizontal webs between tall herbs in relatively open areas.

Leucauge grata (Guérin)

This magnificently coloured *Leucauge* is a shade-loving forest species. It was present most frequently on the well-shaded areas of transect I (58%) and occurred less frequently on transects II (13.4%) and III (14%). The maximum number of six individuals occurred on transect I. On transect II there were never more than two individuals, and on transect III the species was represented by single individuals.

Leucauge immatures

These were present all the year round on all three transects. On transects II and III the majority of these were almost certainly young of *L. papuana*. Large numbers occurred on transect III (range 34–198) and on transect II (range 7–124). The immatures on transect I were probably young of *L. papuana* but some could have been young *L. grata*. Numbers were never as high on this transect (range 1–29).

PSECHRIDAE

Psechrus argentatus (Doleschall)

This spider was first regarded by us as an agelinid because of its large horizontal sheet web which terminated in a cocoon-like retreat. It proved to be a cribellate and was identified as above. The species was common in the Wau valley wherever herb-covered embankments provided suitable web sites. The retreat is commonly built either in rock fissures or at the base of clumps of grass, ferns or woody herbs. The long, relatively narrow sheet may extend up to one metre out from the retreat and is a strong, highly permanent structure. Suitable web sites were most common on transect III, where the species was present all the year round in the greatest numbers (range 15–79). It occurred on transect II on 85% of the censuses (maximum number 21) and less frequently (63.5%) on transect I, where there were never more than 13 individuals. This distribution between transects reflects the differences between the transects in the distribution of sloping banks. Immatures occurred only on transect III, which may therefore have been the only breeding population.

Fecenia sp. (close to *angustatus*)

This interesting spider builds an almost vertical sheet web among the thick stems of herbs, grasses and ferns. The web is superficially orb-like and terminates in a curled-leaf retreat above. It is probably a forest species and occurred most commonly on transect III (90%) where it was also most numerous (maximum 27 individuals). On transect II a maximum number of six individuals occurred and the species was present on only 31% of the censuses. On transect I the species occurred rarely (only on four occasions) and there were never more than two individuals. Immatures of this species produced a more-or-less tented sheet web with a conical silk retreat above. They occurred frequently on transect III.

PHOLCIDAE

? *Pholcus* sp.

In general pholcids seem to prefer dark places and this New Guinea species was no exception. Its distribution was entirely confined to crevices in overhanging rock ledges on transect III. It was present there on 66% of the censuses and reached a maximum abundance of 13.

LINYPHIIDAE

Linyphia sp.

This small black linyphiid, a typical forest-dwelling species, occurred on all transects but was most common and numerous on transect III (72% of censuses, maximum number 10). On the other transects the recorded numbers never exceeded two and occurrences were sporadic (transect II, 17%; transect I, 21%).

Table 4. Web-site preferences of species recorded on each transect.

Species	Transects			Web site preferences
	I	II	III	
Cyclosa insulana[2]	+	+	+	small, within and above herb layer
Cyclosa bifida[2]	−	−	+	
Gasteracantha theisi[2]	+	+	−	small aerial webs
Gasteracantha taeniata[2]	+	+	+	
Argiope aemula[2]	+	+	+	large, within and above herb layer
Argiope picta[2]	+	+	+	
Argiope sp. F[2]	+	+	−	small, within herb layer
Argiope reinwardti[2]	+	+	+	large, within herb layer, rock faces, in shade
Nephila maculata[3]	+	+	+	large aerial webs
Araneus theisi[2]	+	+	+	small, within and above herb layer
Araneus sp. B[2]	−	−	+	
Araneus sp. C[2]	+	−	+	
Araneus sp. D[2]	−	−	+	
Araneus laglaizei[2]	+	−	−	
Poltys illepidus[2]	+	+	+	large aerial, nocturnal
Cyrtophora monulfi[3]	+	+	+	small, within herb layer
Leucauge papuana[1]	+	+	+	horizontal above herb layer
Leucauge grata[1]	+	+	+	
Tetragnatha sp.[1]	+	+	+	
Uloborus sp.[2]	−	+	+	rock faces
Linyphia sp.[2]	+	+	+	small, within herb layer
Fecenia sp.	+	+	+	large, above herb layer
Psechrus argentatus[3]	+	+	+	funnel, on rock faces
Theridiids[3]	+	+	+	small-medium within herb layer
Pholcids	−	−	+	rock faces

1. webs readily destroyed. 2. webs relatively durable. 3. webs very durable.

THERIDIIDAE

Free-living species (i.e., non-kleptoparasites)

Web-building theridiids were recorded from transects I and II on 98% of the censuses and all the year round on transect III. From the appearance of the spider and similarity of web sites and structures we assume that this was probably a single species.

Kleptoparasites

Theridiid kleptoparasites occur in the webs of *Nephila maculata* (at least two species; cf. Robinson & Robinson 1973), the Wau *Argiope* species, and the webs of other araneids. We recorded their presence on 73% of the censuses on transect I, 46% on transect II and 52% on transect III.

Table 4 lists the species recorded for all three transects. Note that the maximum number occurs on transect III and that only two species recorded from either of the other transects are absent from this one. Transect I has five 'absences' and transect II, six. Differences between transects in dominant species are discussed in the section on species diversity (p. 152–154). Table 4 summarises our conclusions about web-site preferences and includes comments on the durability of the webs of the species found on the transects.

PHENOLOGY OF THE SPIDERS

A major reason for undertaking the study was to determine whether spiders living under a relatively benign climatic regime would show seasonality (in reproduction or any other aspect of population biology). Few phenological data are available from tropical areas and most of these are based on studies of vertebrates. Studies of the phenology of tropical arthropods include those of Emmel & Leck (1969) on butterflies of Barro Colorado Island (Panama), Gibbs & Leston (1970) on a wide range of insects in a cocoa farm

Table 5a. Monthly rainfall at Wau Ecology Institute during the census period and average rainfall recorded at other stations in the Wau valley (recorded in mm).

	W.E.I.		Golden Ridges[1]		Wau No. 1[2]	
	Dry	Wet	Dry	Wet	Dry	Wet
Jan.		296.4		190.5		168.7
Feb.		147.1		199.9		194.6
Mar.	134.1			193.3		212.3
Apr.		327.2		214.1		186.9
May	71.6		148.3		124.0	
June	79.8		84.6		87.4	
July	101.4		118.9		111.8	
Aug.	27.7		110.5		109.0	
Sept.	99.8		110.7		125.0	
Oct.		346.0	163.6		139.0	
Nov.		236.0		172.0		194.8
Dec.		272.8		236.5		205.7

1 Mean rainfall based on 12 years records
2 Mean rainfall based on 28 years records.

1 & 2. From Brookfield and Hart, 1966.

(Ghana) and incidental studies of insect abundance by Fogden (1972) in forest (Sarawak). Robinson & Robinson (1970) provided data on seasonal fluctuations in the composition of the prey caught by ***Argiope argentata*** at Barro Colorado Island and (1973) on aspects of the phenology of ***Nephila maculata*** at Wau. Oppenheimer (in press) studied the fluctuations in the numbers of spiders caught in pitfall traps near Calcutta, India. The substance of all the above-mentioned studies is that seasonal variations in animal and plant populations *do* occur in lowland tropics and that in some cases they may be quite pronounced. These studies are all from the lowland tropics. The Wau study, as far as we are aware, is the first study of the phenology of tropical web-buiding spiders to include many species, and the first phenological study of tropical arthropods conducted at middle altitudes.

Table 5b. Monthly rainfall at W.E.I. during the census period and average rainfall recorded at other stations in the Wau valley by from wettest (1) to dryest (12).

	W.E.I.		Golden Ridges[1]		Wau No. 1[2]	
	Dry	Wet	Dry	Wet	Dry	Wet
Jan.		3		5		6
Feb.		6		3		4
Mar.	7			4		1
Apr.		2		2		5
May	11		8		9	
June	10		12		12	
July	8		9		10	
Aug.	12		11		11	
Sept.	9		10		8	
Oct.		1	7		7	
Nov.		5		6		3
Dec.		4		1		2

1 & 2. As in Table 5a.

PRESENTATION OF THE DATA

Comparing the detailed data from the three transects presents a problem in organisation. We here first present details of fluctuations in numbers and species composition on a transect by transect basis and then, in a final descriptive section, attempt to present

Table 5c. Maximum-minimum temperatures recorded in screened building at Wau Ecology Institute, 1967.

	Min. °C.	Max. °C.		Min. °C.	Max. °C.
January	19	30.8	July	No record	
February	18.6	29.25	August	11.7	30
March	19.75	30.8	September	11.7	31.7
April	17.7	29.3	October	13.3	26.1
May	14.4	30	November	11.1	13.3
June	12.2	31	December	No record	

Table 6. Weekly totals per species for

	3.V.1970	10.V.	17.V.	24.V.	31.V.	7.VI.	14.VI.	21.VI.	28.VI.	5.VII.	12.VII.	19.VII.	26.VII.	2.VIII.	9.VIII.	16.VIII.	23.VIII.	30.VIII.	6.IX.	13.IX.	20.IX.	27.IX.	4.X.	11.X.	18.X.
Weeks	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cyclosa																									
insulana	—	4	2	1	1	1	1	—	1	—	3	4	3	2	4	6	4	—	4	1	—	—	—	2	2
bifida	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
immatures	1	—	3	2	4	3	—	—	2	4	2	—	2	1	3	1	2	—	5	2	1	1	2	—	1
Gasteracantha																									
theisi	23	36	28	24	45	21	25	31	36	31	19	24	23	27	24	22	16	21	20	13	14	18	21	20	17
taeniata	1	3	2	2	1	1	1	—	1	1	2	4	1	—	3	—	3	4	3	2	1	—	—	—	1
immatures	9	9	12	15	14	18	11	28	10	15	14	15	22	7	34	25	27	27	26	24	21	17	15	16	12
Argiope																									
aemula	1	1	1	1	1	1	1	1	1	2	1	—	—	1	1	1	3	1	1	—	—	—	—	—	1
picta	1	4	5	6	5	6	4	4	3	5	10	4	4	2	4	6	5	2	7	3	2	1	4	2	3
sp. F	—	—	—	—	—	—	1	—	—	—	—	1	1	1	—	2	1	3	—	1	—	—	2	1	—
reinwardti	1	1	—	—	2	—	1	2	—	1	2	3	3	2	3	4	2	3	4	1	1	1	1	—	1
males	1	1	—	1	—	1	4	1	1	—	1	6	—	3	7	—	2	2	1	—	—	—	—	—	1
immatures	3	3	4	4	2	4	6	9	4	14	4	9	9	3	5	10	4	8	5	3	—	—	5	7	1
Nephila																									
maculata	6	6	—	2	6	2	5	4	3	2	2	2	3	2	2	2	1	1	3	2	4	1	1	—	—
males	5	2	—	—	2	3	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
immatures	5	7	7	9	4	4	5	5	8	5	5	7	3	3	4	4	1	5	2	—	2	1	1	—	—
Araneus																									
theisi	—	2	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sp. B	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sp. C	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
sp. D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
laglaizei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
spp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nocturnal																									
araneids	2	3	1	1	2	—	2	3	1	1	3	1	1	3	2	3	6	3	2	2	—	1	1	—	1
Cyrtophora																									
monulfi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leucauge																									
papuana	1	2	6	3	5	3	2	7	7	9	14	12	7	9	8	8	8	6	2	3	—	2	2	3	2
grata	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	1	1	—	—	—	—	2	1	2	—
immatures	10	2	6	16	12	19	24	13	9	16	21	21	12	9	13	8	6	8	5	3	2	3	2	6	8
Tetragnatha sp.	49	46	18	19	9	54	69	48	18	63	38	24	21	5	20	43	7	15	10	2	2	2	16	8	7
Uloborus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Linyphiids	—	—	—	—	—	—	—	—	—	2	1	—	1	1	1	—	—	—	1	—	—	—	—	—	—
Fecenia sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
immatures	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Psechrus																									
argentatus	6	4	7	8	13	7	4	2	1	3	6	10	4	9	6	2	7	7	6	—	7	6	4	5	8
immatures	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Theridiids	5	10	7	11	10	4	9	15	18	17	17	7	18	9	6	10	6	14	10	13	14	15	14	16	8
Nephila																									
inquilines	—	—	3	6	10	11	16	21	17	14	27	15	6	18	—	19	7	9	31	12	27	13	7	—	—
Pholcids																									
immatures	28	21	32	46	36	48	46	55	33	54	46	52	48	23	59	48	40	48	43	32	26	23	25	29	22
adults	102	125	80	85	112	115	147	139	108	151	147	117	97	97	91	130	79	91	106	55	72	62	74	59	55
Total	130	146	112	131	148	163	193	194	141	205	193	169	145	120	150	178	119	139	149	87	98	85	99	88	77

transect I (May 1970 to April 1971).

25.X.	1.XI.	8.XI.	15.XI.	22.XI.	29.XI.	6.XII.	13.XII.	20.XII.	27.XII.	3.I.1971	10.I.	17.I.	24.I.	31.I.	7.II.	14.II.	21.II.	28.II.	7.III.	14.III.	21.III.	28.III.	4.IV.	11.IV.	18.IV.	25.IV.	
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	
1	4	4	2	3	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	2	—	—	1	3	1	—	68
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
2	3	6	1	2	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	59
21	25	24	10	13	15	15	20	26	25	26	26	28	23	24	24	32	22	28	22	24	30	30	26	21	21	19	1219
—	—	—	—	—	—	—	—	—	1	1	1	1	1	1	1	2	2	4	2	1	1	2	2	—	1	2	63
20	16	26	21	14	13	17	21	16	16	17	13	14	10	10	18	14	10	20	18	21	20	25	20	26	33	35	947
1	—	—	—	—	—	1	1	1	1	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30
3	3	2	3	2	1	1	1	3	5	4	5	5	3	3	3	3	5	7	5	8	7	9	8	4	4	1	210
—	1	1	1	1	—	—	—	2	1	—	1	1	2	—	1	—	—	1	—	—	—	1	—	—	1	—	29
2	1	—	—	—	1	1	2	1	—	—	—	—	—	—	—	—	—	1	1	1	3	—	—	1	2	3	59
—	1	1	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	2	—	—	—	1	—	—	40
4	4	7	8	6	5	15	6	13	17	8	5	5	4	4	9	7	3	5	5	4	3	2	5	3	7	—	290
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	2	5	4	7	84
—	—	—	—	—	—	—	1	1	—	—	—	—	—	1	2	3	8	7	11	13	18	18	12	28	14	11	163
3	9	17	17	21	24	37	40	53	49	78	84	57	68	68	113	85	99	92	107	114	111	106	88	64	58	28	1787
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	—	1	—	—	1	2	—	—	—	—	—	1	1	—	—	1	2	1	—	2	1	—	—	13
—	1	1	—	—	—	—	—	1	1	—	—	—	—	1	3	3	2	1	3	—	4	4	6	2	6	3	87
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
5	8	9	**3**	2	3	3	—	5	4	4	2	1	—	—	1	4	5	3	3	3	4	6	8	6	6	2	231
—	—	4	**2**	3	4	2	3	2	3	2	3	5	5	4	4	5	2	2	—	3	5	3	4	3	2	4	89
14	18	**18**	6	1	12	13	13	27	9	15	21	9	3	3	6	6	7	4	11	27	16	18	13	13	29	13	599
32	**23**	20	14	18	40	46	34	53	43	39	21	28	—	7	15	29	17	62	43	57	13	60	57	36	45	10	1475
—	**—**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	1	1	2	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	13
1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	3
2	2	1	—	4	4	1	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	161
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14	6	7	12	6	8	7	3	7	5	—	3	4	6	6	12	11	12	16	9	11	11	9	6	11	10	6	501
—	—	—	1	1	1	—	—	2	1	—	2	—	—	1	2	—	2	5	2	6	4	6	7	9	3	8	352
43	50	74	53	44	54	85	80	109	91	118	123	85	85	86	147	112	119	121	141	166	150	151	126	106	127	76	3685
82	77	75	49	55	78	78	68	106	95	78	66	74	41	51	72	93	77	137	102	134	102	149	141	131	120	76	4903
125	127	149	102	99	132	163	148	215	186	196	189	159	126	137	219	205	196	258	243	300	252	300	267	237	247	152	8588

Table 7. Weekly totals per species

	3.V.1970	10.V.	17.V.	24.V.	31.V.	7.VI.	14.VI.	21.VI.	28.VI.	5.VII.	12.VII.	19.VII.	26.VII.	2.VIII.	9.VIII.	16.VIII.	23.VIII.	30.VIII.	6.IX.	13.IX.	20.IX.	27.IX.	4.X.	11.X.	18.X.
Weeks	1	2	2	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cyclosa																									
insulana	7	15	31	22	22	34	42	51	53	75	72	52	49	51	69	56	73	60	67	53	58	48	52	54	48
bifida	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
immatures	38	45	33	49	67	67	56	61	75	92	68	75	75	70	76	31	60	52	69	70	56	52	53	72	56
Gasteracantha																									
theisi	14	9	10	8	19	9	13	13	20	15	17	21	8	16	13	11	12	10	7	7	5	10	4	6	7
taeniata	4	4	3	6	5	1	1	4	3	4	1	3	1	1	3	3	2	4	1	3	2	1	1	2	—
immatures	4	10	15	7	6	5	5	2	3	2	3	—	2	8	6	8	9	5	4	9	4	9	6	4	6
Argiope																									
aemula	7	7	8	7	8	14	14	14	11	11	12	9	11	8	9	9	6	7	8	7	18	15	14	8	11
picta	1	3	4	2	2	2	5	7	3	8	5	8	5	8	3	12	10	8	4	2	3	3	3	4	7
sp. F	—	—	—	—	2	1	1	2	1	1	4	7	8	4	4	2	2	1	1	1	1	—	—	1	1
reinwardti	—	1	5	3	1	1	—	3	2	2	4	1	1	1	4	2	2	—	1	—	—	—	—	1	—
males	—	—	—	—	—	1	—	2	2	2	—	1	1	3	2	—	1	—	—	—	—	—	2	—	—
immatures	12	4	11	13	9	13	3	3	14	17	9	8	9	11	18	9	24	8	16	13	9	13	16	12	9
Nephila																									
maculata	6	11	7	9	7	6	5	1	—	—	—	—	—	—	1	—	1	1	1	2	1	—	—	—	—
males	1	3	2	3	—	2	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
immatures	8	12	11	8	8	2	1	2	1	1	1	1	—	—	1	—	1	4	3	—	3	1	—	—	—
Araneus																									
theisi	6	6	—	1	—	1	5	2	—	5	1	1	—	—	3	1	1	—	2	—	1	—	—	—	—
sp. B	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sp. C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sp. D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
laglaizei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
spp.	—	—	—	—	—	—	—	1	1	—	1	1	—	—	—	2	3	3	2	—	—	1	—	2	—
Nocturnal araneids	—	—	1	—	—	—	1	—	—	1	—	2	2	3	1	1	1	1	—	—	—	—	1	1	—
Cyrtophora monulfi	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Leucauge																									
papuana	20	16	18	25	13	15	32	33	32	40	41	25	29	17	46	37	24	16	22	11	11	13	3	7	6
grata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—
immatures	64	7	49	59	52	109	107	81	78	124	90	65	75	67	54	77	29	24	34	28	18	31	29	50	17
Tetragnatha sp.	41	30	18	19	4	21	43	23	8	48	38	10	34	13	51	32	3	1	3	1	4	5	4	5	4
Uloborus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Linyphiids	—	—	—	—	—	—	—	—	—	1	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Fecenia sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	2
immatures	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Psechrus																									
argentatus	8	20	13	7	22	10	9	5	5	18	17	16	18	18	19	13	13	18	15	14	13	10	8	10	4
immatures	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Theridiids	—	3	2	2	4	8	12	19	19	5	15	10	6	9	4	5	19	10	17	14	13	18	3	15	19
Nephila inquilines	—	—	7	16	13	7	5	10	2	1	3	—	—	—	—	—	1	2	5	4	4	—	—	1	—
Pholcids																									
immatures	126	78	119	136	142	196	172	149	171	236	171	149	161	156	155	126	123	93	126	120	90	106	104	138	88
adults	115	128	129	130	122	133	188	191	163	237	231	167	174	155	232	189	174	142	156	119	134	124	95	118	109
Total	241	206	248	266	264	329	360	340	334	473	402	316	335	311	387	315	297	235	282	239	224	230	199	256	197

for transect II (May 1970 to April 1971.)

25.X.	1.XI.	8.XI.	15.XI.	22.XI.	29.XI.	6.XII.	13.XII.	20.XII.	27.XII.	3.I.1971	10.I.	17.I.	24.I.	31.I.	7.II.	14.II.	21.II.	28.II.	7.III.	14.III.	21.III.	28.III.	4.IV.	11.IV.	18.IV.	25.IV.	
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	
62	62	76	69	81	87	88	90	79	69	78	74	61	68	71	57	52	52	67	37	65	73	88	77	68	72	87	3124
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
60	77	83	64	52	44	51	42	43	45	39	40	22	30	37	52	28	27	59	108	69	57	59	48	44	70	96	2964
9	5	4	3	3	4	3	5	4	9	12	11	11	9	13	7	7	4	8	7	10	6	9	4	8	6	4	469
—	—	—	—	—	—	—	—	—	1	1	2	1	2	2	1	2	1	1	1	1	—	1	—	—	1	—	81
6	3	6	7	5	8	8	11	8	8	7	10	10	12	13	23	10	9	7	10	8	11	5	11	3	8	10	379
7	9	6	7	5	4	1	2	3	3	4	5	5	7	6	4	—	1	1	—	—	—	1	1	1	—	1	337
3	3	2	5	3	4	3	2	1	4	1	1	2	2	1	2	3	3	2	2	1	2	1	—	—	1	2	178
—	—	1	—	—	—	2	1	1	1	—	1	2	1	—	2	2	—	1	2	2	2	2	2	—	1	2	73
—	—	—	—	—	—	—	—	—	1	1	3	1	1	1	—	—	—	—	—	1	1	—	—	—	—	—	45
—	1	1	2	—	—	2	—	—	—	—	4	—	3	1	2	—	1	—	—	2	—	1	1	—	—	—	38
13	11	19	6	9	15	21	11	18	18	8	11	11	9	6	10	2	1	4	3	4	3	3	5	2	4	2	512
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	3	1	—	2	—	68
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	1	—	—	1	—	4	1	1	2	3	3	33
3	10	9	6	22	9	21	13	16	41	33	46	41	63	70	97	38	26	21	34	28	21	20	24	19	14	21	835
—	1	—	—	2	—	2	—	1	—	2	—	1	—	—	—	—	—	2	3	1	—	—	—	6	4	2	63
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	1	—	—	20
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17
—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
5	12	6	4	15	12	6	5	27	10	13	11	6	7	6	7	7	6	12	11	14	6	8	5	12	14	11	810
—	—	—	—	—	2	—	1	—	1	—	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	—	9
37	37	52	38	42	45	15	23	46	22	28	8	28	17	28	33	17	7	44	41	93	13	53	97	71	91	61	2505
19	11	24	3	6	23	10	8	27	16	17	4	40	3	5	4	5	—	10	10	19	—	8	22	17	19	25	818
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	1	1	1	—	—	—	—	—	—	—	—	—	1	—	1	2	—	—	—	—	—	1	—	—	—	—	11
—	—	—	—	1	—	—	—	—	1	3	5	3	6	3	3	1	1	—	—	1	1	1	—	—	—	—	34
—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	1	—	—	—	—	6
5	4	4	5	4	3	1	—	1	1	1	1	1	1	—	—	1	1	—	—	1	1	—	1	1	1	1	363
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14	11	14	8	7	7	15	21	19	14	16	11	8	8	9	8	16	30	22	10	20	13	5	5	3	2	5	572
—	—	1	—	—	3	—	2	—	—	—	—	2	—	1	—	2	—	—	1	1	2	—	—	—	—	—	96
119	139	170	121	130	121	116	100	131	134	115	115	112	131	154	216	95	70	135	196	203	105	141	185	139	187	190	7201
124	121	140	107	128	149	133	137	163	131	149	133	145	120	120	101	101	100	127	86	141	113	130	120	119	126	143	7262
243	260	310	228	258	270	249	237	294	265	264	248	257	251	274	317	196	170	262	282	344	218	271	305	258	313	333	14463

Table 8. Weekly totals per species

	3.V.1970	10.V.	17.V.	24.V.	31.V.	7.VI.	14.VI.	21.VI.	28.VI.	5.VII.	12.VII.	19.VII.	26.VII.	2.VIII.	9.VIII.	16.VIII.	23.VIII.	30.VIII.	6.IX.	13.IX.	20.IX.	27.IX.	4.X.	11.X.	18.X.
Weeks	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cyclosa																									
insulana	—	7	4	—	4	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	2
bifida	—	18	23	11	16	17	—	4	7	4	4	5	2	1	—	—	—	1	—	2	—	—	3	1	1
immatures	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gasteracantha																									
theisi	—	1	4	1	1	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	—
taeniata	—	2	2	4	7	5	—	4	5	7	3	5	4	7	6	5	3	4	5	4	4	4	4	1	3
immatures	—	5	2	5	9	3	—	1	—	2	3	3	—	4	2	3	1	1	3	—	1	—	—	2	2
Argiope																									
aemula	—	—	—	—	—	1	—	1	—	—	—	—	—	1	1	1	1	1	1	1	1	1	1	1	—
picta	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sp. F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
reinwardti	—	5	6	13	14	14	—	13	10	11	9	9	9	6	7	8	9	6	4	6	4	6	3	6	7
males	—	—	—	—	—	—	—	1	2	—	1	1	—	—	—	—	—	—	—	—	—	3	1	—	1
immatures	—	56	33	22	29	31	—	28	26	25	19	31	32	24	31	22	37	20	32	15	23	25	32	29	35
Nephila																									
maculata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
males	—	1	—	1	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
immatures	—	15	14	11	22	9	—	13	21	20	15	24	11	16	22	22	12	19	16	28	20	12	17	18	16
Araneus																									
theisi	—	3	2	1	1	—	—	—	—	—	1	1	—	1	1	1	1	—	—	—	—	—	—	—	—
sp. B	—	1	4	6	3	1	—	2	1	1	1	1	—	—	2	—	—	2	—	—	1	—	—	—	2
sp. C	—	1	3	4	1	1	—	—	—	—	—	—	8	4	7	4	2	1	5	6	7	2	1	2	—
sp. D	—	—	1	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
laglaizei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
spp.	—	3	2	2	1	1	—	5	1	3	4	3	1	—	—	1	3	—	1	1	2	4	1	5	—
Nocturnal araneids	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	2	—	—	1	1	—	—	—	—	—
Cyrtophora monulfi	—	—	1	1	1	1	—	2	—	1	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—
Leucauge																									
papuana	—	9	17	19	25	19	—	23	21	17	17	19	18	14	21	14	18	21	15	12	13	17	18	23	27
grata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
immatures	—	60	37	43	108	107	—	106	159	108	141	194	186	143	198	110	110	146	57	39	34	42	69	83	59
Tetragnatha sp.	—	—	7	6	12	14	—	9	8	3	2	6	5	6	7	8	1	3	1	—	3	—	7	9	5
Uloborus sp.	—	21	42	12	31	22	—	11	5	11	4	3	6	9	7	5	1	4	2	2	—	5	5	8	5
Linyphiids	—	9	10	—	2	2	—	—	1	3	3	6	3	3	4	4	3	1	1	3	3	—	3	1	—
Fecenia sp.	—	14	10	4	6	3	—	1	1	5	3	2	3	2	5	2	2	—	—	—	—	1	—	1	6
immatures	—	3	7	4	9	16	—	20	19	16	18	15	14	37	33	30	33	24	17	20	25	25	30	26	27
Psechrus																									
argentatus	—	48	54	55	64	79	—	50	54	45	77	45	38	60	43	46	41	47	54	34	51	30	39	29	34
immatures	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	25	31	41
Theridiids	—	6	16	9	18	8	—	20	21	17	24	21	23	15	21	15	16	26	20	19	16	16	15	25	20
Nephila inquilines	—	—	5	4	—	1	—	4	3	4	6	4	—	—	—	1	—	2	4	1	3	3	1	—	—
Pholcids	—	5	13	4	7	3	—	1	—	8	1	—	—	—	—	—	—	—	—	—	—	1	—	4	2
immatures	—	139	93	85	177	166	—	168	225	171	196	267	243	224	286	187	193	210	125	102	103	115	173	189	180
adults	—	155	226	157	216	193	—	153	141	140	161	131	120	129	134	118	102	120	115	93	108	93	102	117	115
Total	—	294	319	242	393	359	—	321	366	311	357	398	363	353	420	305	295	330	240	195	211	208	275	306	295

for transect III (May 1970 to April 1971).

25.X.	1.XI.	8.XI.	15.XI.	22.XI.	29.XI.	6.XII.	13.XII.	20.XII.	27.XII.	3.I.1971	10.I.	17.I.	24.I.	31.I.	7.II.	14.II.	21.II.	28.II.	7.III.	14.III.	21.III.	28.III.	4.IV.	11.IV.	18.IV.	25.IV.	
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	
2	1	1	—	—	—	—	—	—	—	1	—	—	—	1	1	—	2	—	—	—	—	—	—	—	—	—	28
5	2	3	4	5	6	6	3	2	3	5	3	—	—	9	7	7	3	7	4	5	8	7	9	9	7	7	256
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10
2	3	3	1	1	1	—	—	3	1	—	2	1	4	1	2	—	1	—	—	—	1	1	1	1	1	—	129
1	2	8	4	5	5	5	2	3	3	1	2	—	—	—	—	—	—	—	—	—	1	1	—	—	1	1	97
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	6	7	10	11	8	11	11	16	14	15	16	21	16	16	10	16	15	18	15	25	24	21	22	14	11	13	575
1	2	2	4	—	4	1	1	3	4	—	1	3	3	10	2	4	—	—	—	1	1	2	3	1	—	—	63
45	53	49	54	61	67	66	73	72	59	58	50	57	41	54	46	47	27	48	33	44	27	30	32	20	18	28	1916
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	—	—	1	2	2	2	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	3	2	5	26
23	21	24	23	28	26	28	39	35	39	34	24	33	43	39	47	45	62	41	35	60	54	56	44	54	56	58	1464
—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15
3	3	2	—	—	4	4	5	3	2	1	5	4	1	3	3	1	1	2	3	4	2	4	2	5	3	1	99
3	2	1	6	5	6	2	1	2	3	1	—	2	7	2	5	4	7	7	—	7	4	4	1	2	3	3	149
—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1	—	1	—	1	1	—	1	2	2	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	54
—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	8
—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	1	1	2	1	—	—	—	—	—	—	18
21	28	26	27	25	30	23	33	33	35	21	25	20	21	10	14	11	8	8	12	10	8	16	15	10	13	16	936
—	—	1	—	—	—	1	1	—	1	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	7
117	93	115	49	88	79	78	89	162	47	50	86	85	74	87	136	97	102	111	119	121	35	130	85	65	81	74	4794
13	6	2	5	5	10	8	7	9	3	4	5	3	2	4	—	1	2	6	1	6	5	3	6	7	4	3	252
9	8	9	4	7	9	7	8	9	16	2	6	2	5	7	6	8	7	5	4	12	13	10	10	10	8	4	426
1	—	3	2	3	1	1	1	—	3	—	—	1	4	1	1	2	1	—	—	1	2	1	—	—	—	—	94
6	7	7	9	11	17	10	10	20	21	27	23	26	41	26	26	21	19	14	18	21	23	12	3	7	11	5	512
35	16	21	25	22	25	32	29	30	26	30	30	20	22	25	21	17	14	8	9	2	—	—	—	—	—	—	927
24	28	26	21	15	19	18	19	40	29	33	27	37	43	48	40	49	53	48	43	46	48	39	38	47	42	36	2073
46	59	53	33	47	52	61	49	25	33	38	31	22	25	13	28	17	9	9	8	—	2	3	2	2	2	3	780
23	21	25	27	17	28	28	32	30	21	20	12	18	20	23	26	14	19	15	20	14	8	4	14	11	5	5	907
—	5	1	2	5	2	1	7	2	—	—	—	—	1	—	—	—	—	—	—	—	—	2	—	—	—	7	81
3	—	2	2	5	9	3	7	3	4	—	3	1	—	3	8	6	5	3	2	7	2	4	1	—	1	—	133
267	244	270	188	251	254	270	281	327	207	211	223	217	205	218	278	223	214	217	204	227	119	220	163	141	158	164	9978
126	122	123	125	119	157	126	150	178	163	130	129	141	169	164	151	144	144	135	126	160	149	130	128	127	111	105	6871
393	366	393	313	370	411	396	431	505	370	341	352	358	374	382	429	367	358	352	330	387	268	350	291	268	269	269	16849

Table 9. Yearly totals by species plus weekly means, ranges, standard deviations and standard errors of the means, for each transect.

	I	II	III	I			II			III			I	II	III
	Yearly Totals			Weekly Means	S.D.	S.E.	Weekly Means	S.D.	S.E.	Weekly Means	S.D.	S.E.	Range		
Cyclosa															
insulana	68	3124	28	1.3	1.6	0.2	60.1	18.8	2.6	0.5	1.3	0.2	0–6	7–90	0–7
bifida	—	—	256	—	—	—	—	—	—	5.1	4.9	0.7	—	—	0–23
immatures	59	2964	—	1.1	1.5	0.2	57.0	18.0	2.5	—	—	—	0–6	22–108	—
Gasteracantha															
theisi	1219	469	10	23.4	6.3	0.9	9.0	4.4	0.6	0.2	1.4	0.2	10–45	3–21	0–4
taeniata	63	81	129	1.2	1.1	0.2	1.6	1.5	0.2	2.6	2.0	0.3	0–4	0–6	0–7
immatures	947	379	97	18.2	6.6	0.9	7.3	3.8	0.5	1.9	2.1	0.3	7–35	0–23	0–9
Argiope															
aemula	30	337	13	0.6	0.7	0.1	6.5	4.5	0.6	—	—	—	0–3	0–18	0–1
picta	210	178	1	4.0	2.1	0.3	3.4	2.5	0.4	—	—	—	1–10	0–12	—
sp. F	29	73	—	0.6	0.7	0.1	1.4	1.6	0.2	—	—	—	0–3	0–8	—
reinwardti	59	45	575	1.1	1.1	0.2	0.9	1.2	0.2	11.5	5.3	0.8	0–4	0–5	3–25
males	40	38	63	0.8	1.4	0.2	0.7	1.0	0.1	1.3	1.8	0.2	0–7	0–4	0–10
immatures	290	512	1916	5.6	3.5	0.5	9.8	5.5	0.8	38.3	15.3	2.2	0–17	1–24	15–73
Nephila															
maculata	84	68	—	1.6	1.9	0.3	1.3	2.5	0.4	—	—	—	0–7	0–11	—
males	163	33	26	3.1	0.6	0.8	0.6	1.1	0.1	0.5	1.0	0.1	0–28	0–4	0–5
immatures	1787	835	1464	34.4	38.4	5.3	16.1	19.9	2.8	29.3	14.9	2.1	0–113	0–97	11–62
Araneus															
theisi	3	63	15	—	—	—	1.2	1.7	0.2	0.3	0.6	0.1	—	0–6	0–3
sp. B	—	—	99	—	—	—	—	—	—	2.0	1.6	0.2	—	—	0–6
sp. C	6	—	149	—	—	—	—	—	—	3.0	2.4	0.3	—	—	0–8
sp. D	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—
laglaizei	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
spp.	13	20	54	—	—	—	—	—	—	—	—	—	—	—	—
Nocturnal															
araneids	87	17	8	—	—	—	—	—	—	—	—	—	—	—	—
Cyrtophora															
monulfi	1	2	18	—	—	—	—	—	—	—	—	—	—	—	—
Leucauge															
papuana	231	810	936	4.4	3.1	0.4	15.6	10.7	1.5	18.7	6.8	1.0	1–14	3–46	8–35
grata	89	9	7	1.7	1.7	0.2	—	—	—	—	—	—	0–5	—	—
immatures	599	2505	4794	11.5	7.0	1.0	48.2	28.7	4.0	95.9	41.0	5.8	1–29	7–124	34–198
Tetragnatha sp.	1475	818	252	28.4	19.0	2.6	15.7	13.4	1.9	5.0	3.3	0.5	0–69	0–48	0–14
Uloborus sp.	—	1	426	—	—	—	—	—	—	8.5	7.3	1.0	—	—	0–42
Linyphiids	13	11	94	—	—	—	—	—	—	1.9	2.1	0.3	—	—	0–10
Fecenia sp.	5	34	512	—	—	—	0.7	1.3	0.2	10.2	9.5	1.3	—	0–6	0–27
immatures	3	6	927	—	—	—	—	—	—	18.5	10.1	1.4	—	—	0–37
Psechrus															
argentatus	161	363	2073	3.1	3.3	0.5	7.0	6.8	0.9	41.5	13.5	1.9	0–13	0–22	15–79
immatures	—	—	780	—	—	—	—	—	—	15.6	19.5	2.8	—	—	0–61
Theridiids	501	572	907	9.6	4.2	0.6	11.0	6.4	0.9	18.1	6.6	0.9	0–18	0–30	4–32
Nephila															
inquilines	352	96	81	6.8	7.9	1.1	1.8	3.3	0.5	1.6	2.1	0.3	0–31	0–16	0–7
Pholcids	—	—	133	—	—	—	—	—	—	2.7	3.0	0.4	—	—	0–13
Adult females*	3225	6373	6530	62.0	18.1	2.5	122.6	26.1	3.6	130.6	26.2	3.7	31–101	92–170	90–219
Immatures	3685	7201	9978	70.9	40.7	5.6	138.5	44.1	6.1	199.6	45.1	6.4	21–166	70–236	85–327
Total	8588	14463	16849	165.1	55.1	7.6	278.1	54.6	7.6	337.0	62.2	8.8	77–300	170–473	195–505

**Tetragnatha* sp. not included.

the between-transect fluctuations. Table 5 gives monthly totals for the rainfall at the Wau Ecology Institute site and details of the mean annual temperature ranges for the district. More detailed temperature records, and hours of sunlight data, are desirable in a study such as this but we were unable to obtain them. In interpreting rainfall data and their possible correlation with the fluctuations in the numbers of web-building spiders, Robinson & Robinson (1973) have suggested that the whole subject is fraught with complications and that simple daily or weekly totals may be of little value. The same authors also point out that rainfall in areas of strong relief may vary considerably at localities separated by as little as half a mile. Transects I and II were sufficiently close to the W.E.I. rain gauge to be unaffected by this factor but caution must be exercised in the case of transect III.

Our raw data consist, for each transect, of weekly numbers totalled for each census unit (10 metre long division) and for the whole transect. Most workers on spider phenology have presented data on numbers per fortnightly period (e.g., Merrett 1968, Russell-Smith & Swann 1972) or computed spiders per day for the actual trapping period (Merrett 1968, for instance). Other workers (e.g., Duffey 1962) have quoted monthly totals. (Monthly totals are given for Emmell & Leck's butterfly data and Fogden's insect data.) Tables 6, 7, and 8 give the weekly totals, per species, for transects I, II and III, respectively, and the yearly (across-row) totals. Table 9 gives, for each transect, the yearly totals by species plus means (weekly), ranges, standard deviations and standard errors of the means. It also includes similar data for the totals of adults, immatures, and adults+ immatures for each transect.

Monthly and "seasonal" totals are used in the accompanying figures where appropriate. We also inculde figures scoring presence or absence on a weekly basis.

ANALYSES OF DATA AND THE CLASSIFICATION OF SEASONAL PATTERNS

The detailed interpretation of population curves undoubtedly involves the use of more sophisticated climatological data than are available for the Wau area. It has been widely assumed (see Richards 1957) that rainfall and temperature data are sufficient to delimit seasons in tropical areas. There is recent evidence, however, that other climatological factors may influence the seasonality of organisms. Thus Gibbs & Leston (1970) have shown that at Tafo (Ghana, West Africa) six seasons can be delimited by using rainfall and hours of sunlight data, and that the seasons thus defined permit a more useful interpretation of insect phenology than is possible by using rainfall/temperature data alone. The limited temperature data available for Wau (together with our subjective impressions) suggest that annual variations in temperature are small and that these are probably unimportant to most organisms. The amount of variation in hours of sunlight and light intensity throughout the year remain unknown.

Faced with inadequate climatological data, we have, albeit crudely, divided the year into the six wettest months and the six driest months. This division is based on the rainfall of the census year. Two months, April and March, fall into seasons that differ from those in which they would be placed if the long-term distribution of monthly rainfall were used to delimit seasons (see Table 5). These 'arbitrary' seasons are referred to as wet and dry, without implying that they are necessarily different enough to be biologically real.

To analyse our data for distributional trends related to these two 'seasons' we plot-

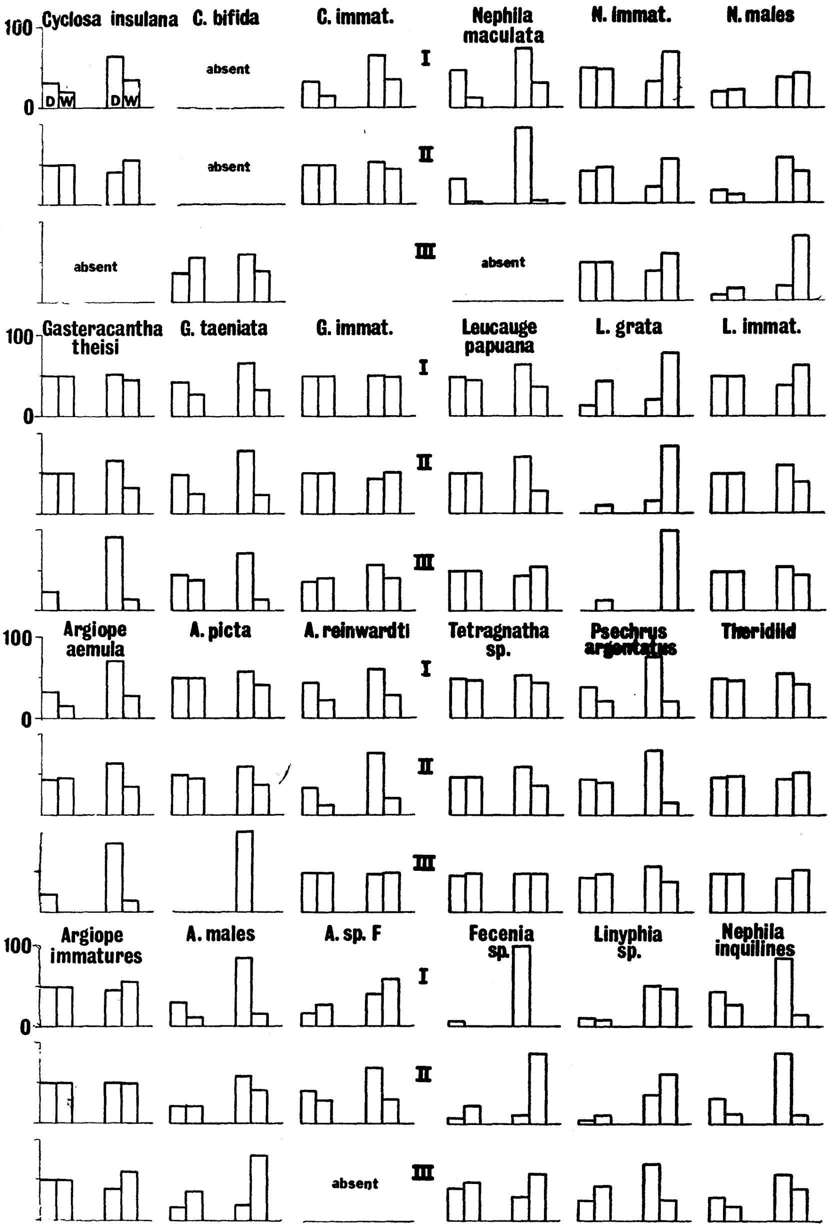

Fig. 5. Distributions of common species on the three transects during wet (W) and dry (D) seasons: the first two bars show percentages of weeks (52 weeks=100%) during which a species was present, during the dry and wet seasons; the second two bars show the percentages of total numbers of each species divided between the dry and wet seasons (total number of individuals per species per year=100%).

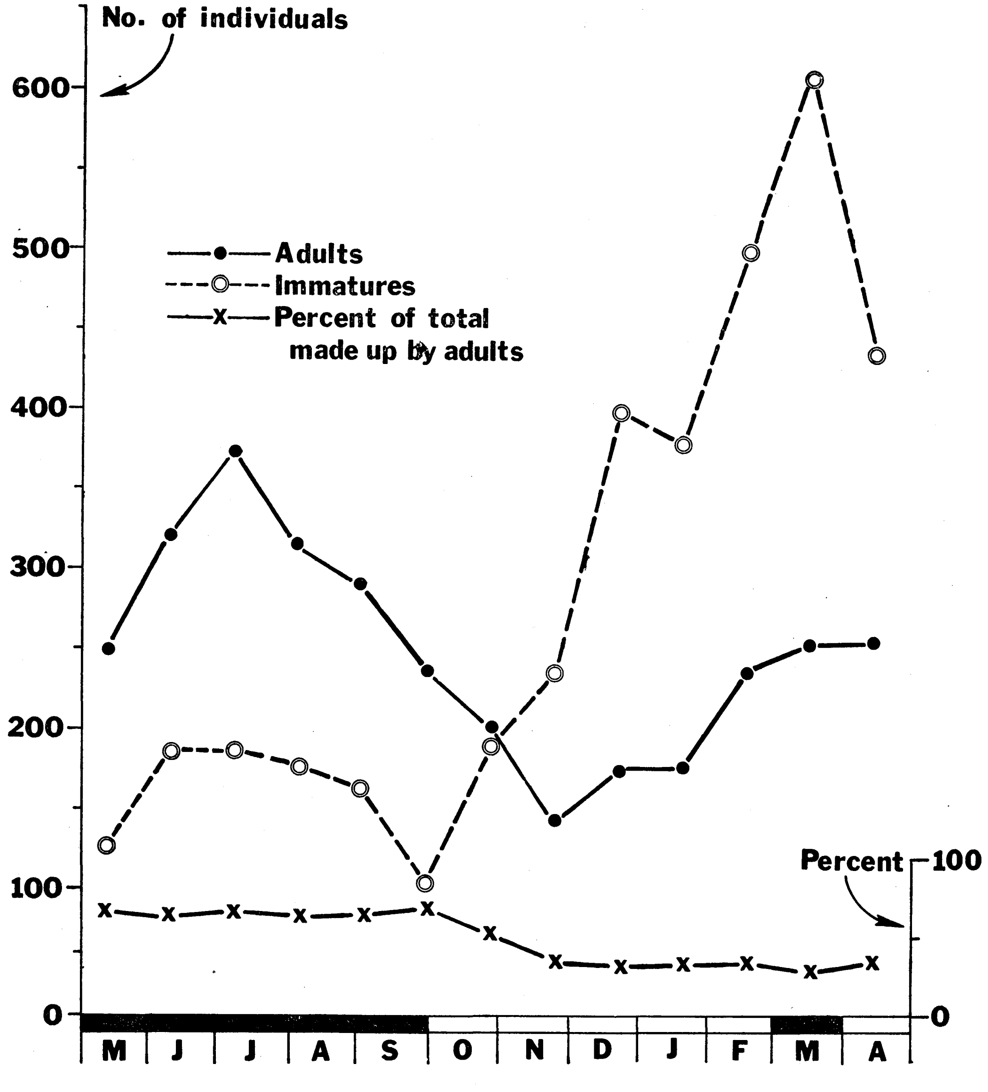

Fig. 6. Total numbers of adults and immatures of all species combined on transect I, and percentage of total made up by adults of all species.

ted for each transect the fortnightly totals as histograms for all species represented by an annual total of more than thirty. As a guide to interpretation in dubious cases (most species showed fairly clear-cut population trends when graphed), we inserted a line at the level of 10% of the maximum fortnightly total for the species. These 'working graphs' are not included herein since they would involve a disproportionate amount of space. We found that plotting the percentage distribution of numbers divided between wet and dry seasons shows the overall distributional trends (without showing the distributional peaks) in a relatively condensed form and these graphs form the basis for Fig.

5, alongside histograms showing the percentage 'seasonal' distribution of occurrences (simple presence or absence). Cases where both numbers and presences occur markedly in one season are listed below according to season. Cases where the species is present throughout the year are classified as year-round, and seasonal peaks, if present, are noted. Rare species are ascribed to seasonal or sporadic categories either from the raw data (if less than 30 per year) or from analysis of the graphs. In dubious cases our classification is intuitive and non-statistical.

TOTAL NUMBERS OF SPIDERS, TRANSECT I

The highest monthly averages of adult spiders occurred in the period March to September, the drier months of the census year (excluding an aberrant April, see Table 5). The highest weekly counts of adults occurred in the first week in June (103) and the third week in July (109). The lowest counts, 32 and 34, were made in two successive weeks in December. (In these totals we have excluded *Tetragnatha* sp. since the variance of these was very great, see Table 6.) From October to mid-February, the number of adult spiders never exceeded 60 per week. This seems to be a distinct seasonal effect and is clearly visible in Fig. 6. Combining species (that probably possess different habitat preferences) does not mask the fact that high numbers occur during period of relatively low rainfall.

Immatures increase markedly in numbers as rainfall increases. The average number of immatures was always below 60 during the dry months (excluding March which was aberrant, see Table 5). This trend probably reflects additions to the immature population from hatchings of eggs. We believe that only a small proportion of the weekly count of immatures was made up by individuals that had emerged and been counted at earlier censuses. (The greater proportion of immatures were always at hatchling size. Mortality after emergence and dispersal must be very high indeed; the egg-masses of many araneids contain from 200 to over 1000 eggs). The development period of the eggs of the species occurring on the transects is not known, but studies of *Argiope argentata* in Panama show that spiderlings may disperse as soon as 22 days after the eggs are laid. On the other hand, it is also known that spiderlings may remain within the egg-cocoon, after hatching, until their emergence is triggered by favourable conditions. Thus, one of the species at Wau, *Nephila maculata*, has been studied in the Bombay region of India. There, according to Thakur & Tembe (1956), young appear in August, seven months after the last adults were seen; thus the young have spent more than 5 months in the cocoon. (Thakur & Tembe were obviously mistaken in assuming that these young were hatchlings as they reported that they were 1 cm. long). For these reasons it is difficult to deduce anything about the possible peaks in egg laying from the data on emergence of immatures (assuming that we are right in ascribing peaks in immature populations to emergences).

In the course of a year we counted 4903 adult spiders and 3685 immatures on this transect. (Note that these totals must include many individuals that are present on successive censuses.)

NUMBERS OF SPECIES, TRANSECT I

Table 10 gives the number of species encountered on each transect per week of the census. For this purpose we scored *Nephila* kleptoparasites as one species, although, in fact, there are two (Robinson & Robinson 1973). Both 'unidentified' and 'nocturnal' araneids are each scored as one species, although there may well have been more than one involved in each case. Most of the variation results from the sporadic presences of the 'rare' species as can be seen from Fig. 2, 3 & 4. Table 2 details some events that could have affected census results (tree falls, grass cutting, very heavy rain, etc.) with dates, so that these can be cross referred to the census data.

Note that for all transects the average number of species is higher in the six drier months than in the six wetter months. The greatest differences in averages occur on transect II, the most exposed of the three. Transect III has the greatest number of species. In fact, there are more species at the lowest average (during the six wettest months) on transect III, than on the other transects at their highest averages. In overall terms, the variations in species number over the year are very minor indeed and the overall impression is one of general stability. This picture is modified if numbers of individuals and presence of immatures are included in the analysis.

TEMPORAL VARIATION OF NUMBERS OF INDIVIDUALS, TRANSECT I

Studies of spiders of the North Temperate region generally show that they have discrete periods of activity within the year and can be neatly classified on this basis (see Russell-Smith & Swann 1972: 102). In the situation at Wau no such pattern is immediately obvious.

Following the analytical system described on p. 144, the following species are regarded as *all the year round in distribution*:

Gasteracantha theisi — adults and immatures
Argiope picta — adults
Argiope immatures
Argiope species "F"
Leucauge papuana — adults and immatures
Tetragnatha sp.
Theridiid
Linyphiid

Of these *Gasteracantha theisi* is numerous all through the year, with a lowest fortnightly count of 24. The population size, although variable, does not show any seasonal trends. Immatures peak after adult peaks (i.e., at the end on the dry season and at the end of the wet).

Argiope picta adult females are present in low numbers throughout the year and peaks in numbers show no patterned trends. *Argiope* immatures (a category which could comprise the young of four species) are present throughout the year without major peaks in numbers.

Adults of *Leucauge papuana*, present more-or-less throughout the year, occur in slightly greater numbers during the dry season as do the immatures of this species.

Tetragnatha sp. occurs throughout the year but with very considerable variation in numbers. This variation, as noted earlier (p. 144), may be due to the fragility of *Tetragnatha* webs and consequent censusing problems. If anything, there are more spiders present in the dry season, but the difference is not very great considering the large total number involved.

Theridiids are present all-the-year round and show no marked seasonal trends (in this case we may have confounded adults and late-stage immatures and this will tend to mask any weak seasonality).

The following species are not consistently present all-the-year round, and have *essentially dry season distributions:*

Argiope aemula — adults
Argiope reinwardti — adults
Argipoe males (very marked seasonality)
Nephila maculata — adult females
Psechrus argentatus
Fecenia sp.
Cyclosa insulana — adults and immatures
Nephila inquilines

Of these seasonal species ***Argiope aemula*** and ***Argiope reinwardti*** are never abundant and transect I must be regarded as a peripheral habitat (see Section I). This is probably also true of ***Cyclosa insulana*** and is certainly true of ***Nephila maculata*** which was absent for most of the wet season on transect I but was present for the whole year in the adjoining woodland (see Robinson & Robinson 1973a).

The following species are seasonal and have ***essentially wet season distributions:***

Leucauge grata
Nephila maculata — immatures
Nephila maculata — males

Although transect I is the one on which we encountered most specimens of ***Leucauge grata***, the wet season trend is confirmed by data from the other two transects (see later) and the species is an essentially shade-loving forest form. Data from the adjoining woodland (Robinson & Robinson 1973) confirm the peaking of ***Nephila*** males during the late wet season.

TOTAL NUMBERS OF SPIDERS, TRANSECT II

The pattern of numbers distribution on this transect peaks for adults, during June, July, August and September with the highest weekly totals in July (189, 193). May (a dry month) has the lowest monthly total and one week has the lowest weekly total (74). Apart from one week in March, no other weekly total falls below 80. Transect II thus has higher weekly totals throughout the year than transect I. Interestingly, there was a second (minor) peak in numbers during the mid-wet season when numbers were very low on transect I. See Fig. 6 & 7.

Immature spiders are present in large numbers throughout the year. They peak at the onset of dry conditions and rise to a similar peak at the end of the following wet season (i.e., by April, normally part of the dry season; see Table 5).

In the course of the year we counted 7262 adult spiders on this transect and 7201 immatures.

NUMBERS OF SPECIES, TRANSECT II

As noted earlier, this transect has the greatest difference between the mean number of species present in the dry months compared with the mean present in the wet months. The highest number of species recorded from this transect was 18 (recorded for the week ending August 16th, the lowest number of species occurred in October when only 9 species were recorded for the week ending October 25th.

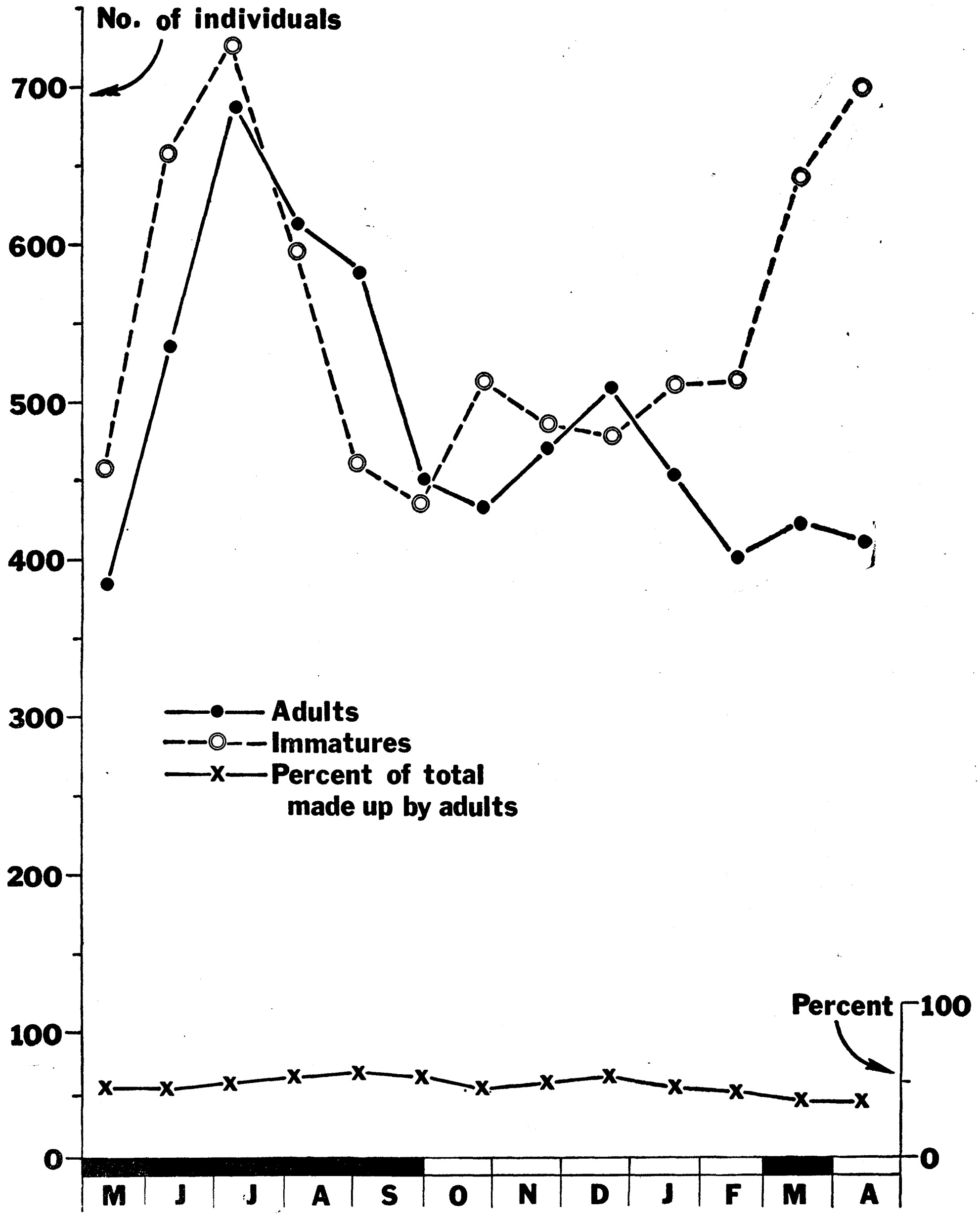

Fig. 7. Total numbers of adults and immatures of all species combined on transect II, and percentage of total made up by adults of all species.

TEMPORAL VARIATION OF NUMBERS OF INDIVIDUALS, TRANSECT II

The following species are regarded as ***all the year round in distribution:***

Cyclosa insulana — adults and immatures
Gasteracantha theisi — adults
Gasteracantha immatures
Argiope aemula — adults
Argiope immatures
Tetragnatha sp.
Theridiid
Leucauge immatures
Nephila inquilines

Of these, *Cyclosa insulana,* the most numerous araneid on this transect, varies very little, showing a very slight peak in the mid-wet season. *Cyclosa* immatures occur in bursts throughout the year, once again suggesting that hatching occurs intermittently throughout the year. *Gasteracantha theisi,* although never absent, peaks in the dry months and drops to its lowest population level in mid-wet season. Immature *Gasteracantha* reach a slightly higher population level in the wetter months.

Both *Argiope aemula* and *A. picta* reach higher population levels in the dry months than in the wet months but are probably best regarded as aseasonal, and immatures of these, and perhaps *A. reinwardti,* have a markedly uniform distribution and are therefore, in all probability, hatching in all months.

Leucauge immatures (contrast with adults later) are present in good numbers all the year round but peak in mid-dry season. They are thus very seasonal in distribution, although the peaks do not obviously correlate with any single factor.

The following species have very clear-cut peaks and ***essentially dry season distributions:***

Gasteracantha taeniata
Argiope reinwardti
Argiope species "F"
Nephila maculata — adult females
Leucauge papuana — adults
Psechrus argentatus

Of these, it is possible to attribute some apparent seasonality to rarity effects (thus the first four are represented by less than 100 individuals) but this is clearly excluded as an explanation for the distribution in time of numbers of *L. papuana* and *Psechrus argentatus.* The horizontal webs of *Leucauge* sp. could be regarded as susceptible to damage by rain to a greater extent than the other araneids on this particularly exposed transect.

Other spiders have a ***markedly wet season distribution.*** These include:

Nephila maculata — immatures
Leucauge grata (very rare)
Linyphiid (very rare)

The last two cases can probably be dismissed since very small numbers are involved (less than 12 individuals in each case). The case of *Nephila maculata* immatures, on the other hand, is very striking indeed and the wet season peak is very pronounced.

Note that males of *Nephila maculata* and *Argiope* sp. occur very sporadically but with some tendency to a dry months concentration.

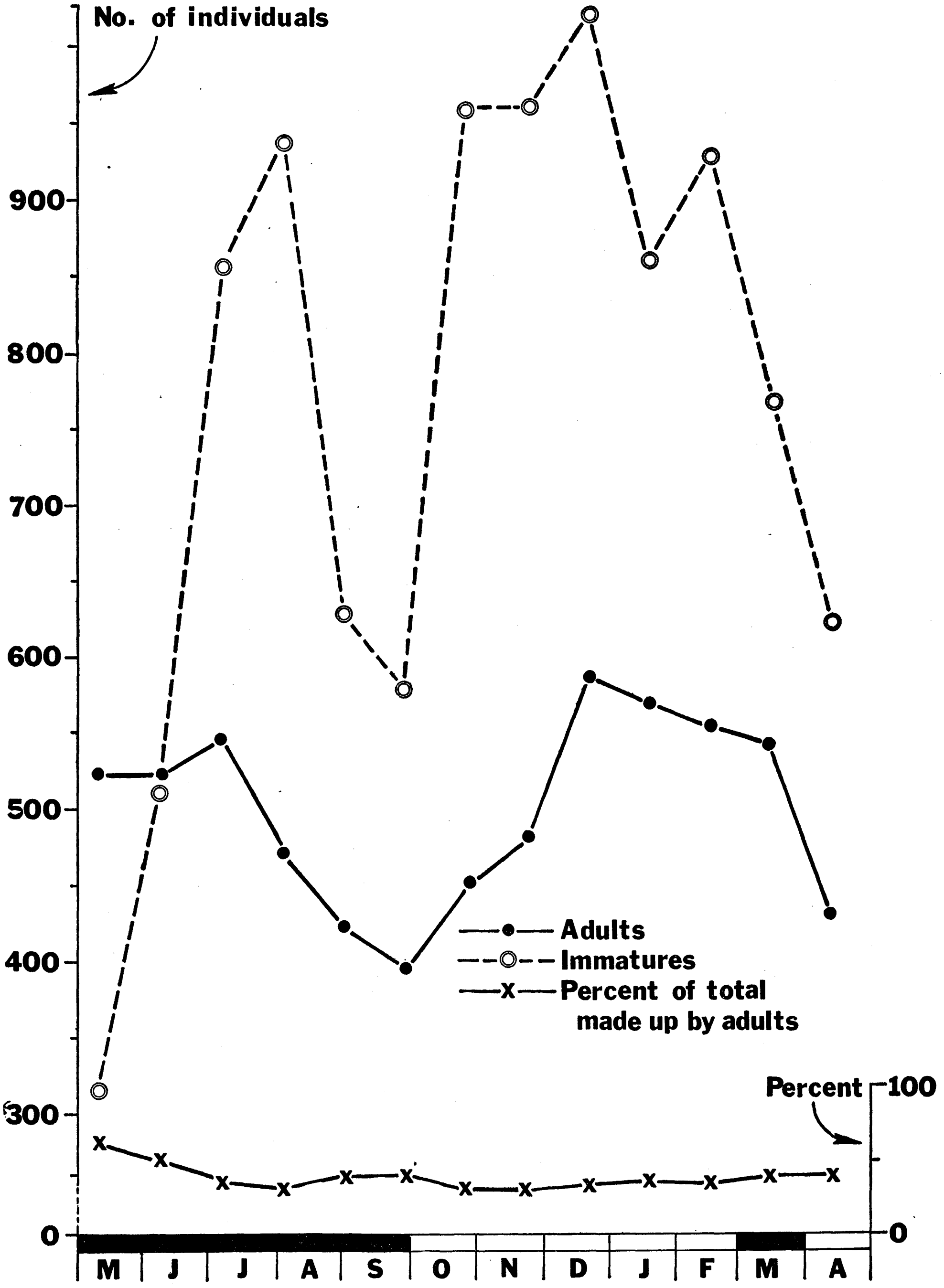

Fig. 8. Total numbers of adults and immatures of all species combined on transect III, and percentage of total made up by adults of all species.

TOTAL NUMBERS OF SPIDERS, TRANSECT III

Transect III differs from the other two transects in that the peak adult populations occur in three of the wet months, December, January and February. The month with the fourth highest score is March (normally a wet season month; see Table 5). The lowest weekly scores occur in two weeks in September and the first week in October; all are less than 100 (93, 93, 95). At no other time in the year does the weekly score fall below 100. Thus the variation in adult numbers on transect III is less than that on transect II (see Fig. 8).

The census of immatures regularly involved very high scores, although there are two distinct peaks, one in mid-dry season and a higher and more sustained peak in mid-wet season.

In the course of a year we counted 6871 adults and 9978 immatures.

NUMBERS OF SPECIES, TRANSECT III

The mean number of species recorded during the dry months (16) is only slightly higher than the mean for the wet months (14.9). The highest number of species recorded at any census was 20 (two weeks in May) and the lowest 12 (April).

TEMPORAL VARIATION OF NUMBERS OF INDIVIDUALS, TRANSECT III

The following spiders are regarded as ***all the year round in distribution:***

Cyclosa bifida — adults and immatures not separated for census purposes
Uloborus sp.
Argiope reinwardti — adults
Leucauge papuana — adults and immatures
Tetragnatha sp.
Psechrus argentatus
Theridiid

Of these the *Argiope reinwardti* adults show some tendency to a wet season peak (this would be pronounced if March were a wet season month). *Psechrus argentatus*, although present in quite high numbers all the year round, in fact has a bimodal distribution in the year, the wet season peak being lower than the mid-dry season one. *Uloborus* sp. is present all the year round but reaches maximum numbers during the dry months.

Spiders that are absent for part of the year with ***a markedly dry season distribution*** include:

Argiope aemula — adults
Gasteracantha theisi — adults
Gasteracantha taeniata — adults and immatures
Nephila inquilines

All of these are relatively rare spiders on transect III, with only *Gasteracantha taeniata* exceeding 100 individuals in yearly total.

The following species have ***intermittent distribution and wet season peaks:***

Argiope sp. males (probably *A. reinwardti*)
Nephila maculata males
Leucauge grata (very rarely encountered)

Two groups of immatures are numerous on an all the year round basis but have striking wet month peaks. These are ***Argiope*** and ***Nephila*** immatures.

PHENOLOGY: SYNTHESIS AND DISCUSSION

Some interesting comparisons emerge when all three transects are considered. Adults on all transects peak in numbers during the third four-week period of the census (see Fig. 6, 7, 8) and this is the highest peak of the year for the transects lying roughly at the same altitude (I & II) but is exceeded by the scores of the second dry-season peak on the higher transect III (where four successive four-week totals exceeded the July peak). On transect I, the peak in adults comes approximately 32 weeks before the peak in immatures, whereas, on transect II, the peak of adults coincides with a peak of immatures and is also followed, approximately 36 weeks later, by a second peak of immatures. On transect III both peaks of adult spiders are accompanied by roughly coincident peaks of immatures, and these are approximately 20 weeks apart. Detection of long-term trends would require a study over a longer period than one year, but it is tempting to

Table 10. Number of species encountered on each transect per week of census period.

	Transect			
Week	I	II	III	
1	12	10	—	
2	13	12	18	
3	12	13	21	
4	12	13	18	
5	13	13	21	
6	11	14	19	
7	14	14	—	
8	11	15	17	dry
9	12	12	14	
10	14	14	16	
11	15	15	17	
12	13	15	15	
13	15	13	13	
14	15	14	14	
15	13	14	16	
16	15	17	17	
17	15	16	15	
18	13	14	16	
19	14	15	16	
20	12	12	16	
21	11	13	14	
22	13	11	13	
23	13	10	15	
24	9	15	16	wet
25	13	10	13	
26	11	9	16	
27	12	13	14	
28	12	13	19	
29	11	10	14	
30	12	12	16	
31	11	11	16	
32	11	11	16	
33	10	11	19	
34	14	11	17	wet
35	16	14	17	
36	8	13	13	
37	11	13	13	
38	10	15	15	
39	9	15	14	
40	13	13	15	
41	14	12	14	
42	10	13	13	
43	10	10	16	
44	12	12	13	
45	11	12	14	
46	12	15	14	dry
47	12	11	14	
48	11	12	15	
49	12	9	14	
50	12	10	12	wet
51	13	11	13	
52	11	11	13	

	Transect I	Transect II	Transect III
Mean, dry season	12.85	13.58	15.96
wet season	11.54	11.81	14.81
Yearly mean	12.2	12.69	15.38

Note that nocturnal araneids, *Araneus* spp. and *Nephila* inquilines are scored as single species.

think that the situation on transect I is relatively simple and that the peak of immatures that we detected towards the end of our study was the result of the reproductive activities of the peak of adults present at the beginning of the study and would give rise to a similar peak of adults at a later stage. This would involve maturation in about 16 weeks if the pattern followed that of the previous period. On transect II, the situation is more complex and the coincident peaks of adults and immatures, at the start of the study, would require the prior occurrence of similar coincident peaks if the (perhaps simplistic) explanation for the cycle in transect I were extrapolated. At the end of the study period there was a peak of immatures without a coincident peak of adults, so that the following July might not be expected to have a coincident peak. It is noteworthy that the interval between the adult peak in July and the second immature peak period in April is only four weeks longer than the interval between these peaks on transect I. The situation on transect III is even more complicated and the interval between successive peaks of immatures is short. This transect, at a higher altitude than the other two, was consistently more humid, and this condition may allow for more continual hatching of eggs and dispersal of spiderlings.

The proportion of adults (less ***Tetragnatha*** sp. and all males) to immatures is shown on Fig. 6, 7, 8, and in Table 11. These data are of considerable interest. Duffey (1962) reported variations in this figure that range from 48% to less than 7%. Only on transect I was there variation of this magnitude and there the proportion of adults never fell below 29.6% (for four-weekly totals). Transect II had the smallest differential of 18.6% with a range of from 37.1% to 55.7%. Transect III had a range from 32.2% to 62.2% (differential 30.0%).

On transect I, the proportion of adults is remarkably constant over the first six four-weekly periods of the census (dry months) ranging from 63.3% to 69.8%. It then falls to a fairly constant lower level, in one step, and remains between 30% and 40% during the wet months, reaching its lowest point in the 'aberrant' dry month of March.

On transect II, the variation ranges between 43.8% and 55.7% during the 11 four-weekly periods up until the 'aberrant' dry month of March, *where again the proportion reaches a low point*. The lowest point on this transect occurs in the month following the unusual dry period.

On transect III, there is a low point in mid-dry season and a second one, the lowest, in the four-week period immediately after the end of the dry season. In interpreting the pattern on this transect, it must be remembered that the rainfall data from the Wau Ecology Institute may not exactly reflect rainfall conditions at the higher site.

The overall picture that emerges from consideration of totals and proportions reflects the relatively crude nature of these data. There are obvious sources of confounding in lumping data from a number of species but nonetheless, it seems reasonable to conclude that the spiders are, in the main, living in benign conditions that permit year-round maintenance of large populations and reproductive activity. Despite this, considerable fluctuations still occur in some species.

Species by species comparisons are perhaps more useful and revealing.

Cyclosa insulana occurred on all three transects but was rare on transect III where it was essentially replaced by *Cyclosa bifida*. On transects I and II *Cyclosa insulana* was present throughout the year, but with a dry season tendency where it was less numerous (transect I). On transect II, where this was the numerically dominant araneid, both adults and immatures were virtually aseasonal. This is an interesting situation in so far as transect II, the most exposed of the three transects, presumably was the most susceptible to climatic (micro- and macro-) fluctuations. *Cyclosa bifida* was similarly aseasonal on transect III. The high population level of *C. insulana* maintained on transect II (mean of 0.3 per square metre per week, adults and immatures) suggests that there was a year-round availability of small insects and that hatching is not greatly influenced by relatively dry conditions.

Gasteracantha theisi adults and immatures were aseasonal on transects I and II and very rare on transect III, where *G. taeniata* was the dominant *Gasteracantha*. When *G. theisi* occurred on transect II it was found on the edge of the adjacent woodland where conditions were presumably very similar to the greater part of transect I and where the species was the preponderant araneid in numbers. Considering that the webs of this species are aerial (with frames spanning woody plants above the ground rather than in the herb layer) and relatively delicate, the absence of marked seasonality is striking. Building inside forest may insure some protection against the worst effects of wind and rain.

Argiope aemula is the dominant species of *Argiope* on transect II and rare to very rare on the other two transects. On transect II it was present all the year round but with peak numbers in the dry season. The species is roughly similar in size to the New World *Argiope argentata* and fairly similar in ecology. It is interesting to note that the latter species is greatly reduced in numbers during the dry season in Panama (Robinson & Robinson 1970). The species builds its large, strong webs in the open where it would be least protected from rain or wind damage, but this seems to be an improbable explanation of the dry season peak in numbers on transect II.

Argiope picta, the dominant *Argiope* species on transect I, is aseasonal there and on transect II is more or less present all the year round but with a dry season bulge in numbers and occurrences. Here there may well be a tendency for a shelter-loving species to exploit peripheral habitats when conditions are relatively dry. The virtual absence of this species on transect III may be associated with the dominance of *Argiope reinwardti* at that location. The latter species is relatively rare on transects I and II, where it occurs principally in the dry season. On transect III *A. reinwardti* occurs all the year round with little seasonal variation in numbers.

Argiope immatures, present all the year round on transects I and II, show no seasonal fluctuation, except for a slight increase during the wet season on transect I, where they are, in all probability, mainly *A. picta* immatures (adults of *A. picta* outnumbered the other two species combined by nearly 4 to 1). On transect III the very numerous immatures (here almost certainly *A. reinwardti*) were present all the year round but peaked in numbers during the wet season. This distribution is interesting because of the very marked seasonality of *Nephila maculata* immatures (see below) and the absence of marked seasonality in numbers of adult *A. reinwardti*. This latter fact suggests that seasonality of hatching, or emergence, or both could be a factor of importance.

Nephila maculata adults were never numerous on transects I and II and altogether absent on transect III. The spider is, however, a large one and some conclusion can be drawn from the fact that the occurrences are largely confined to the dry season. Immatures were numerous on all three transects and clearly peak in the wet season. The source of these immatures on transect III must have been the adjoining forest and their seasonal distribution suggests that even in forest conditions, populations of this spider may fluctuate seasonally (for further evidence of this see Robinson & Robinson 1973). An interesting facet of the biology of this species is illustrated by the fact that adult males occurred on transect III despite the fact that no adult female was recorded there. These males were found on the webs of sub-adult females and occurred largely during the wet months, as did the more numerous males on transect I.

In general *Araneus* species were rare on all three transects but transect III consistently had more species and individuals than the others. Two of these species, species "B" and "C," were non-seasonal in occurrence; the others were too rare for comment. On transect II, one species, *Araneus theisi*, was predominantly a dry season form.

Leucauge papuana was found quite abundantly on all three transects, occurring all the year round on the shaded transects I and III and as a dry season species on transect II. *Leucauge* immatures occurred all the year round on all transects, peaking in the wet months on transect I and twice without relation to season on transect II. These immatures were very abundant on transect III with no seasonal peaks.

Fecenia sp. was rare on transects I and II and quite common on transect III where it clearly occurred more abundantly during the wet months. *Fecenia* immatures were abundant on transect III, although they were absent in April and the numbers were low in March and May. *Psechrus argentatus* occurred as a dry month species on transects I and II and all the year round on transect III. On that transect adults had two peaks of the population and immatures peaked in the wet months.

On all transects theridiids and *Tetragnatha* sp. were present all the year round without apparent seasonality. *Uloborus* sp. was not recorded from transect I, occurred once on transect II and was fairly abundant on transect III where the population peaked during the dry months.

Table 11. Percentage of adult females on each transect per 4-week period.

4-week period	Transect I	Transect II	Transect III
1	66.3	45.6	62.2
2	63.3	44.8	50.6
3	66.7	48.6	38.9
4	63.9	50.6	33.5
5	64.0	55.7	40.2
6	69.8	50.7	40.6
7	51.9	45.6	32.0
8	37.4	49.1	33.4
9	30.6	51.5	36.4
10	31.5	47.1	39.8
11	32.0	43.8	37.4
12	29.6	39.6	41.4
13	36.8	37.1	40.9
Range	29.6–69.8	37.1–55.7	32.0–62.2
Differential	40.2	18.6	30.2

A number of workers who have studied the phenology of North Temperate region spiders have pointed out that different stages in the life history of spiders may be restricted to different habitats (see Edgar 1971, for instance). We have no means of excluding this possibility in assessing our data although araneids may well be considered less mobile, after initial dispersal, than the hunting spiders that form the subject of most other studies. Only in the case of transect III do we know fairly definitely that some immatures (*Nephila maculata*) were derived from areas outside the transect, since no adults occurred there during the census period. The transects were all on edges of fairly extensive areas that were potential sources of immigrants and a margin (accumulation) effect is certainly possible in many cases. It is also possible that some spiders moved into transect areas from more preferred habitats when populations in those habitats reached a high level or when conditions were otherwise unfavourable. The dry season occurrence of *Nephila maculata* on transects I and II certainly coincides with peak populations of adult spiders of this species in adjoining areas. This may well be the case for other spiders with markedly seasonal distribution. A purely speculative listing of these invaders would include:

Leucauge papuana (on the open transect II) Dry season
Leucauge grata (all transects) Wet season
Gasteracantha taeniata (all transects) Dry season
Psechrus argentatus (transects I and II) Dry season
Argiope aemula (transect I) Dry season
Argiope reinwardti (transects I and II) Dry season

These species are listed in descending order of our conviction about the validity of this explanation, and in no case do we feel that this is likely to be the only explanation of the seasonality that we observed.

In a recent extremely interesting study, Fogden (1972) has shown that a group of largely insectivorous birds in equatorial rain forest in Sarawak are as markedly seasonal in breeding behaviour as birds in North Temperate regions. This seasonality exists in an environment where there is remarkably little seasonal variation in climate. It is also an area where available estimates of the abundance of several groups of insects suggests that variation in the abundance of these is only a "few-fold", compared with "several thousand-fold in temperate woodland" (Fogden 1972: 339). Fogden ascribes the seasonality in bird behaviour to the existence of variation in food supply. The spiders at Wau are, of course, insectivores and the available data (Robinson & Robinson 1973), obtained in a study area close to our transects I and II, suggest that variation in insect numbers is only a few-fold and is not markedly seasonal. It is quite possible that variations in the numbers of adult and immature spiders that show seasonal trends (as detailed above) may be related to variations in food supplies that have not been detected by insect sampling methods. It is also possible that the very different resources used by immature spiders (very small insects in the main) show a greater seasonality than the resources used by larger spiders and that these variations have not been detected so far. Small insects with relatively short life cycles may be intrinsically more susceptible to the influence of very minor climatic variations. A seasonality of immatures could impose a seasonality on adults, even if the latter had a fairly constant available food supply. The elucidation of this possibility requires data that are more detailed than those currently available.

A phenological study of tropical butterflies led Emmel & Leck (1969) to postulate the existence of a "Seasonal Ecotone." They argue that the joint exploitation of a seasonal transition period by species from communities that are appropriate to each of the adjacent seasons may well be a general phenomenon. Our data on fluctuations in the number of species present on the transects do not show any trends that can be interpreted as evidence for a seasonal ecotone. This could be due to the fact that we have insufficient climatological data and cannot define the periods of seasonal transition with sufficient accuracy. On the other hand, it is probable that if such overlap of species occurs, it is most readily detectable where seasons are very distinct. In fact Emmel & Leck found evidence of the postulated seasonal ecotone only in clearing species and not in forest species, even though both groups were studied at the same locality (Barro Colorado Island, Panama.) The changes involved in the seasonal transition are almost certainly less pronounced ("cushioned") within the forest. We suspect that slowly developing animals, such as spiders, may be less able to exploit relatively short-term climatic variations than butterflies. The pupal stage in the life history of the butterflies must provide the potential for synchronisation of adult activity with optimum climatic conditions. (And the very great differences between the ecology of butterfly larvae and adults presumably allows this group to develop much more complex temporal strategies than are available to spiders.)

GENERAL DISCUSSION

SPECIES DIVERSITY, ENVIRONMENTAL RIGOR AND SUSTAINED COEXISTENCE

Biologists working with a wide variety of organisms and using data from an extensive range of habitats, climatic and zoogeographic regions have, relatively recently, been greatly concerned with questions of differential faunal diversity.[4] There have been numerous attempts to quantify (by the development of a diversity of indices) the differences in the number of species, with or without relation to the number of constituent individuals, that occur in different communities.

Solutions to the problem of defining and quantifying species diversity are not presently agreed upon. Hurlbert (1971) has commented that species diversity has "been defined in such various and disparate ways that it now conveys no information other than 'something to do with community structure'; species diversity has become a nonconcept." Whatever may be wrong (in terms of imprecision, confounding or sheer biological unreality) with existing definitions (and indices) of species diversity, there is a very real set of phenomena at the core of the subject. This core was simply described by Slobodkin & Sanders (1969) as follows: "the number of species in a collection with a fixed number of individuals is not a random variable over the face of the globe." Accepting differences in faunal diversity as real (even if the magnitude of these differences cannot, as yet, be expressed in a wholly satisfactory way) leads to the question of how the differences can be explained.

Many biologists have suggested that there is a correlation between the structural complexity of the habitat and its species diversity. There is some quantitative evidence that structurally more complex habitats have greater species diversities (for example, MacArthur & MacArthur 1961, MacArthur 1972, Pianka 1967, Abele 1973). Table 3 shows that on the basis of complexity of available web sites transect III was the most diverse. This is the transect that had the highest average number of species present, the highest absolute number, and the highest number of species represented by 52 individuals, or more, during the census year. The differences in web site complexity between the transects are not very great, nor are the differences in species richness by any of the above measures. In terms of year round (resident species?) transect II has the most species (8), closely followed by transects I & III (7).

If, as a purely arbitrary criterion, species represented by at least 52 individuals are regarded as ecologically important, transects I and II have more such species in common than either has with transect III. Transect III has seven such species not shared with transect I and eight not shared with transect II.

Use of information-theoretical indices of species diversity clearly produces results that

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[4] Most of the references in this section contain extensive bibliographies.

are sensitive to seasonal changes in community composition (see Table 12). If censuses are carried out at different times of the year on organisms with unknown reproductive cycles the use of these diversity indices for comparisons can clearly give rise to spurious conclusions.

Until more is known about the biology of the species that we encountered on the transects speculation about the general theoretical significance of seasonal changes in species numbers would, we feel, be premature. The differences between the numbers of species on the transects are indeed slight and, at the best, no more than slightly suggestive of a correlation between species diversity and web site complexity. Since there are, as far as we know, no studies of populations of web-building spiders in other areas more general comparisons are impossible. Nonetheless we feel that there are aspects of the overall phenology of the spiders on our transects at Wau that can be usefully related to the discussion on the origins of biotic diversity. In essence we would argue that the condition of year-round coexistence of many web-building species (at all developmental stages) is a present day reflection of a biological situation that, in the past, would favor the development of high faunal diversity. This view is developed in detail below in relation to some of the theories that have been proposed to account for differential species diversity.

Table 12. Species diversity indices for sample weeks during the census year and for the whole year, for each transect.

Transect	Week 8		Week 35		Totals for year	
	H Brillouin	H^1 Shannon/Weiner	H Brillouin	H^1 Shannon/Weiner	H^1base 2	H^1base 10
I	2.4593	2.6382	2.1628	2.4425	2.97	0.90
II	2.9665	3.1442	2.1594	2.3493	2.83	0.86
III	2.8572	3.0863	2.9879	3.2598	3.27	0.99

A number of theories account for differential species diversity with causal explanations involving effects additional to those of structural complexity. Some of these theories apply to between-habitat diversity situations but the ones examined below can be (and have been) applied to within-habitat differences. Sanders (1968) reviews and extends a classification of such theories originally used by Pianka (1966). We here concentrate on two of these together with two related (and derived) theories developed by Sanders (1968) and Slobodkin & Sanders (1969). The two basic theories that we review here are (as summarized by Sanders 1968: 266):

A. ***The competition theory*** (Dobzhansky 1950, Williams 1964).—Natural selection in higher latitudes is controlled by the physical environment, while in lower latitudes biological competion[5] becomes paramount. This formulation is altered by Sanders (ibid; 267) to state that in environments of high physiological stress, selection is largely controlled by physical variables, but in historically low stress environments natural selection results in biologically accommodated communities, derived from past biological interactions

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[5] To categorise Dobzhansky's viewpoint as a competition theory does it less than justice. He states (1950: 220) "Where physical conditions are easy, interrelationships between competing and symbiotic species become the paramount adaptive problem".

and competition.

B. *The theory of climatic stability* (Klopfer 1959, Fischer 1960, Dunbar 1960, Connel & Orias 1964). — Because of the greater constancy of resources, environments with stable climates have more species than do environments of variable or erratic climates. This theory is generalized by Sanders (1968: 267) to the statement that the more stable the environmental parameters the more species are present.

Both these theories can be interpreted as being dependent on assumed differences in speciation and extinction potentials between environments.

Sanders (1968) proposed a *stability/time* hypothesis to account for within-habitat differences in marine benthic diversity. This theory assumes that there are some habitats where physiological stresses have been historically low, due to environmental stability. In these environments a biologically accommodated community has been free to evolve. On the other hand in environments historically subject to fluctuating physical conditions physically-controlled communities have evolved. (Note that much of this argument is explicitly developed by Dobzhansky 1955 - particularly see p. 221).

Slobodkin & Sanders (1969) propose a further (and partly complementary) theory that relates species diversity to environmental predictability. Although this theory places emphasis on predictability rather than relative constancy it assumes that in "benign conditions of long term predictability" the situation will be one where "biological interactions give rise to biological accommodation" (ibid.: 91).

Throughout the following discussion we will use the terms physically controlled and biological accommodation (and derivatives) without qualification. The assumptions contained in the concepts of biological accommodation and physical control (in relation to community ecology) are largely unproven but we think that they are at least biologically realistic.

All the above hypotheses are to a greater or lesser extent complementary and contain common assumptions. The environmental stability, stability-time, and environmental predictability hypotheses all assume that species diversity is greatest in communities that are relatively free from the restraints imposed by physical instability (long and short term) or unpredictability, or both. In the absence of such restraints high species diversity is attained largely through the process of biological accommodation (the competition hypothesis in its extended form). One aspect of the process of biological accommodation has been underemphasised. Given historical stability (or long term predictability) differences in intra-annual stability are potentially of great importance. In existing communities such differences should be *detectable* in the extent of the *sustained coexistence* of community members. This view can be illustrated from the situation on our transects at Wau, and by making some assumptions (based on our general experience) about the situation under different climatic regimes. Thus:

1. On each of the transects at Wau seven to eight species were present on a year-round basis. Eggs of these species hatched, and were probably laid, in all months of the year. Immatures at various stages of development were present all the year round. In this situation there is a very sustained potential for competitive interaction between individuals and species, and there are year-round interactions with predators, prey, parasites and symbionts.

2. Our observations in lowland Panama suggest that in comparable forest-fringe habi-

tats many web-building spiders appear as immatures at the beginning of the wet season (April-May) and the first adults do not then appear until July-August. The coexistence of species at all developmental stages may thus occur, at the most, for three-quarters of the year. Interactions of the type detailed above (1.) may be restricted to this period. (Peters 1955, in incidental notes, provides data suggestive of a similar seasonal pattern for some araneid species in El Salvador).

3. Data on the phenology of web-building spiders in temperate regions are not readily available (there are a number of single-species accounts of natural history). We would guess that for spiders of comparable size to those of our Wau sample the total period of activity is less than half a year. (For instance, in Britain, *Araneus diadematus*, very generally speaking, appears as juveniles in May, is adult by August, and lays eggs and dies-off by September-October).

Given that there is long-term climatic stability in these regions, then:

At Wau not only are the restraints at a relatively low value but the opportunities for biological interactions are sustained in duration (Fig. 9a). In Panama there is suggestive evidence that conditions in the dry season constitute a period of stress. Nonetheless conditions there are more favorable to sustained coexistence than they are in temperate regions. The actual level of sustained coexistence (now) is assumed to reflect the potential occurring in the past and to be a reflection of a possible diversity producing factor that affected the developing fauna during its evolution. It is also important to stress that not only do periods that are inimical to spiders (winter, dry season) result in cessation of activity but they also affect the period of temporal overlap of these species, their predators and prey during the following favorable season (Fig. 9b & c). (Note that we are using the above examples to compare the possible effects of different climatic regimes on 'conditions of life'. For this purpose we can ignore area effects, insular effects, and the different zoogeographic histories of New Guinea, Panama and Britain. For the purposes of our argument the examples could equally well be regarded as hypothetical.) We would argue that part of the emphasis of the stability/time, and related explanations of differential species diversity needs to be placed on intra-annual stability. This emphasis we regard as additional to, not in place of, emphasis on historical stability. Stressing intra-annual stability — reflected in patterns of species coexistence — leads to the following predictions:

1. Latitudinal comparisons of species diversities in habitats of similar structural complexity will yield the greatest differences when the low latitude habitats have a high degree of sustained coexistence.

2. There will be within-habitat differences in species diversity in the same geographical region if there are climatic differences between these habitats that are detectable in patterns of sustained coexistence.

3. Such differences will be consequent on differences in the extent of biological accommodation. In the case of web-building spiders the degree of biological accommodation should be measurable in terms of the diversity of web structures, web-operating strategies, predatory repertories, anti-predator adaptations, and in the complexity of intraspecific behaviour and the range of associated symbionts and parasites.

From this it follows that investigations of ***patterns*** of species coexistence could be a

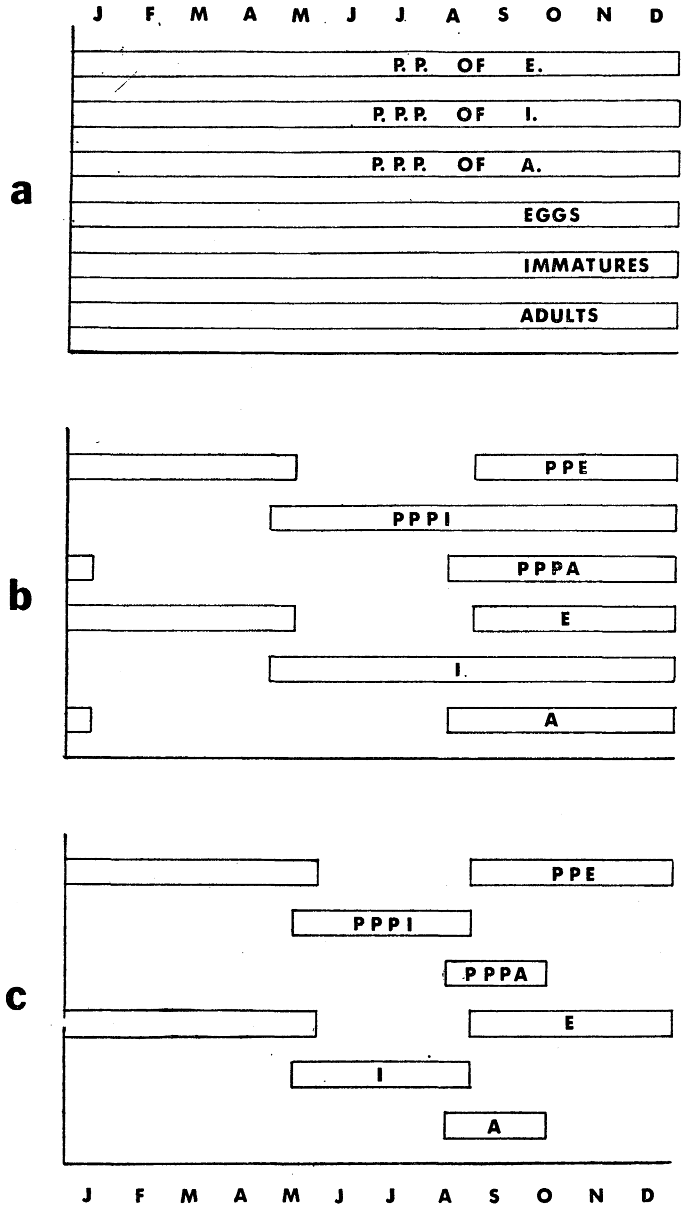

Fig. 9. Temporal overlap of various stages in the life cycle of a spider and its parasites, predators and prey in: (a) the Wau valley transects, New Guinea; (b) Panama (monsoon forest); (c) temperate region forest. PPE=predators and parasites of eggs. PPPI=predators, parasites and prey of immatures. PPPA=predators, parasites and prey of adults.

useful tool for students of faunal diversity. Such studies could be of value both in discovering high diversity situations and in elucidating the causal factors involved. The stability/time, competition and climatic stability hypotheses all postulate diversity-producing processes that would be sensitive to differences in intra-annual stability.

All the theories that seek to account for differential species diversity assume that the factors that they emphasise operate in the situation "other things being equal". We have not, in the above argument, repeatedly emphasised this qualification but would stress it here. We do not doubt that the effects of coexistence on the degree of biological accommodation are affected by the overall framework of the community situation, i.e., by the daily/seasonal/annual physical or environmental stresses, by structural diversity and historical zoogeographic factors. It is thus possible that sustained coexistence may occur within the framework of conditions that severely limit the extent of biological accommodation in the community. Such severe limitation may occur, for instance, in environments subjected to recurrent daily physical stresses. In the marine intertidal zone the stresses resulting from tidal action may block the possibility that complex biological accommodation can occur. (Species may coexist for sustained periods but be able to interact with each other for very limited periods of the tidal cycle). Such environments may be physically controlled irrespective of latitude. Grasslands may be another case in point. These environments may be highly predictable but still be low diversity situations.

Despite the above-mentioned exceptions it is still, in all probability, reasonable to suppose that predictable environments will, in general, favor high diversity compared to unpredictable environments. However, within predictable environments those that are predictably benign for long periods of each year should, we argue, be high diversity situations compared to those that are (equally) predictably benign for shorter periods. Predictability *per se* may be of importance only in contrast to unpredictability.

We have so far avoided consideration of what is meant by predictability. It is a truism to state that all the animals living in a habitat will not be affected by the same elements of environmental variability in the same way, or to the same degree, but this fact must be considered in any treatment of environmental predictability. Further even if it is possible to categorise some environments, at some crude meteorological level, as predictably constant or inconstant, there are a whole range of intermediates where classification is extremely difficult. For example, the extent of year to year variations in seasonal climatic changes in tropical lowlands is poorly documented. There is even less information on how these variations affect organisms. Since meteorological predictabilty is only the starting point and the predictions that are actually expressed in the responses of animals are largely unstudied it will be some time before most tropical environments can be categorised along the predictable-unpredictable continuum.

The problems associated with the general phenomenon of differential species diversity are vast. They clearly cannot be solved through the study of simple systems alone. We suspect that at least some of the problems associated with the origins (and maintenance) of high species diversity communities will prove to be more accessible to solution on land and in the tropics, and particularly through the study of communities where coexistence is most sustained. We are convinced that the solution of the general problem will necessitate an integrated biological study and cannot be achieved by population sampling and statistical analysis alone.

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