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# Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data

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The prey caught by mature female *Argiope argentata* was censused over a period of one year. Ten webs (when available) were examined five times each day, at two-hourly intervals, between 09.00 and 17.00 hours. The prey-animals seen in the webs were classified into orders and lower taxa, where possible. The results of this study are described and discussed.

CONTENTS



## INTRODUCTION

An experimental study of the predatory behaviour of the spider *Argiope argentata* (Fabricius), revealed a differential responsiveness to various types of prey (Robinson, 1969; Robinson & Olazarri, in press). In particular this spider discriminated between Lepidoptera and all other insects. Butterflies and moths were immediately restrained by biting whereas other insects were enswathed in silk and then bitten. Such a discrimination is probably highly adaptive since lepidopterans, by virtue of their wing scales, are able to escape quickly from spiders' webs (Eisner *et al.*, 1964), and the immediate bite applied to these insects is probably more efficient in preventing escapes than the enswathing technique applied to other insects. To find out whether, under natural conditions, *Argiope argentata* includes a substantial proportion of Lepidoptera in its catches, we undertook a census of prey captures.

As far as we know, this is the only study of spider prey which has encompassed a period of 12 consecutive months, and the only one carried out in the tropics. Studies of the prey of orb weavers from north temperate regions are fairly extensive ((see Kajak 1965*b*) for an excellent bibliography). They do not, however, seem to have involved any spiders as large as *Argiope argentata*, and sampling has necessarily been restricted to a much shorter period (largely because of the effects of winter). The effect of the dry season on tropical organisms is a subject of considerable interest to biologists and our studies provide an approach to this problem from a previously unexplored angle.

## MATERIALS AND METHODS

The prey census was carried out on mature female *Argiope argentata* living in the laboratory clearing at the Barro Colorado Island research station of the Smithsonian Tropical Research Institute, Canal Zone, Panama. Each day, at two-hourly intervals from 09.00 to 17.00 hours, we censused the prey present in the webs of ten spiders. Pilot observations showed that the spiders completed their webs between sunrise and 09.00 hours each day. Sunset is between 18.00 and 19.00 hours throughout the year. Our census period was, therefore, one which covered most of the day. We also found that all but the smallest prey were fed upon for more than two hours and feel that sampling at two-hour intervals enabled us to count the greater proportion of the spiders' food. (Insects of less than 0·015 g may have been caught and digested within the two-hour period.) In making the census we did not remove the captured prey or disturb the spiders in any way. We simply carefully examined the prey package(s), situated at the hub or in the capture area, and made a broad taxonomic determination. Thus, we were able to group the prey into orders, and, in most cases, into lower taxa (suborders, superfamilies, families, etc.). We also recorded estimates of the size (length in inches) of some insects although we did not approach closely enough to the webs to measure the prey. The non-disturbance of the spiders and their webs ensured that their prey capture efficiency was unimpaired by our census activities.

The survey was carried out during the period November 1967 to November 1968. Individuals spiders were not marked, each web under census had a numbered stake placed nearby and when the spider moved its web site the stake was moved. When a spider disappeared altogether, another spider in the clearing was assigned the same number. We only observed predation on spiders on two occasions and do not know, in most cases, whether spiders which disappeared were eaten, moved outside the study area, or simply died. For a period during the 1968 dry season (see later p. 351 and Fig. 1) we had less than ten spiders in the study area. We do not know whether this period represents a genuine absence of adult *Argiope argentata* on Barro Colorado Island or whether the spiders moved to undetected sites in the nearby forests. In the 1969 dry season, which was unusually wet, the spiders persisted in the clearing up until the time of writing (14 April).

Special attention was given to captures of Lepidoptera (the initial reason for the study). We soon found that it was possible to score Lepidoptera escapes as well as captures. When we found a web which had signs of insect disturbance in the forms of holes, broken radii and tangles in the viscid spiral, we scored an insect escape (unless the spider was feeding on a newly acquired prey). If in addition to these signs we found large numbers of lepidopteran wing scales adhering to the viscid spiral, we scored a lepidopteran escape. It is conceivable that some distasteful butterflies and moths are

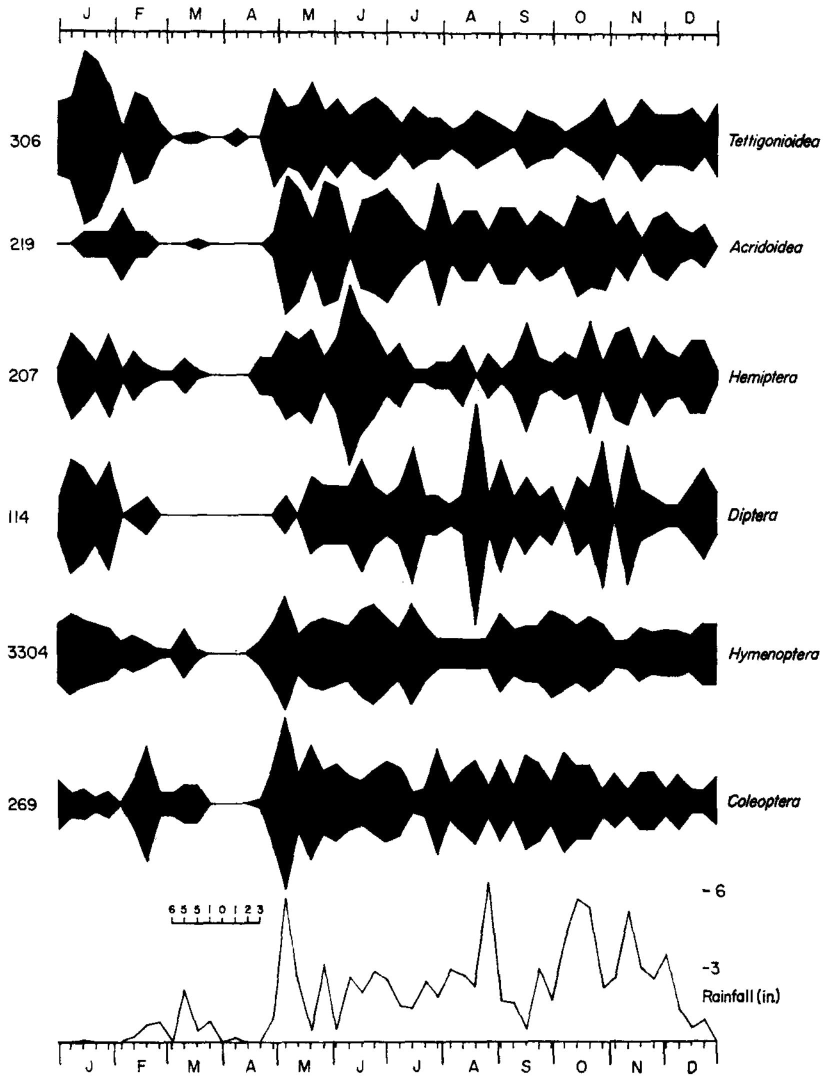


FIGURE 1. Weekly fluctuations in the prey caught by mature female *A. argentata*. Each week's plot on the graphs represents the percentage of the year's catch (of the Order concerned). The rainfall graph is derived from data obtained from a rain gauge situated in the study area. The small scale between the prey capture graphs and the rainfall graph indicates the number of spiders present during those weeks of the dry season when the sample was less than ten.

rejected by *Argiope argentata* and that the signs of rejection, in the web, might be similar to those which we interpreted as evidence of escapes. However, this possibility is not likely to have seriously biased our results since we have not yet found any commonly occurring lepidopterans which are rejected by *Argiope argentata*.

## RESULTS

### *General factors affecting the results*

In order to interpret the results of our study certain important aspects of the behaviour and ecology of *Argiope argentata* must be borne in mind. The nature and composition of the vegetation in the study area is also clearly of importance since it may affect the range of potential prey types available to the spiders.

Wherever we have encountered *Argiope argentata* in Panama, it has proved to be a spider of low vegetation. We have not seen the spider in vegetation exceeding 2 m in height. It is thus a species of forest clearings and road or trailside vegetation. We have not found *Argiope argentata* in extensive grassland areas, although we expected to do so. Its webs are seldom built to a height of more than 50 cm above the ground and are almost always inclined to the vertical (although always more nearly vertical than horizontal). The spider stands at the hub of the web and on the underside. The upperside of the web usually faces clear areas or areas of lower vegetation. The webs vary in size from day to day and from spider to spider. Such variations may depend on the predatory success of the spider (see Witt (1963) for a review of the effects of food supply on web size in araneids). Webs are not always provided with a new viscid spiral each day. The spider may tear down the old spiral and replace it one or more days later or it may keep the old spiral for a day or two without renewal. Strangely enough when the web is without a viscid spiral the spider may continue to sit at the hub and even build a new stabilimentum (Robinson & Robinson, 1970).

On Barro Colorado Island adult *Argiope argentata* are present throughout the greater proportion of the year, and during our census were totally absent from the study area during one week only. Reproduction occurs intermittently throughout the whole year and we recorded adult males in, or near, female webs in each calendar month.

In the course of our census we recorded data on prey captures for 2614 new webs and 195 old webs. In 55 cases the spider rested on a web with no viscid spiral—a web incapable of trapping prey. (Note that during the dry season 399 webs were missed since we were without our full sample of ten spiders. During the rest of the year individual spiders were missing or constructed no web at all on 277 occasions and on 11 days—110 potential webs—we were not present to make the census.)

The dominant floristic element of the study area is composed of grasses which reach a height of up to 1 m with a number of flowering plants and shrubs interspersed. Of the herbs three members of the Piperaceae are dominant, two *Piper* species and *Pothomorphe peltata* (L.), these appear to flower more or less all the year round and are visited in large numbers, as a pollen source, by stingless bees (mainly of the genus *Trigona*). Plate 1 shows the general aspect of part of the study area.

### *Prey captures*

The total catch of insects of all types is shown in Table 1. From this it will be seen that bees constituted by far the largest number of insects caught (2910). These were almost entirely stingless bees of the genus *Trigona* and were occasionally caught in very large numbers by individual spiders. They constitute 62% of the total catch and

Table 1. The prey caught by a sample population of mature female *Argiope argentata:* yearly totals for the various prey categories, percentages and estimated wet weights (see text). In this Table and Tables 2 and 3 figures appearing in the row opposite the ordinal name refer to prey which could not be classified into lower taxa

| | Total no. | % of total (by no.) | Estimated wt of a single insect (see text) (g) | Estimated wt of prey caught (g) | % of total (by weight) |
|---|---|---|---|---|---|
| *Odonata* | | | | | |
| Anisoptera | 46 | 0·1 | 0·26 | 12 | 4·8 |
| Zygoptera | 2 | 0·04 | 0·4 | 0·09 | 0·03 |
| *Orthoptera* | | | | | |
| Grylloidea | 8 | 0·2 | 0·18 | 1·4 | 0·6 |
| Tettigonioidea | | | | | |
| under 0·5 in. | 190 | | 0·136 | 25·8 | |
| 0·5–1·5 in. | 114 | 6·5 | 0·53 | 60·4 | 30·6 |
| over 1·5 in. | 2 | | 0·84 | 1·7 | |
| Acridoidea | | | | | |
| under 0·5 in. | 123 | | 0·122 | 14·9 | |
| 0·5–1·5 in. | 85 | 4·7 | 0·439 | 37·3 | 24 |
| over 1·5 in. | 11 | | 0·74 | 8·1 | |
| *Hemiptera* | 23 | 0·5 | 0·07 | 1·6 | 0·6 |
| Homoptera | 28 | 0·6 | 0·06 | 1·7 | 0·7 |
| Heteroptera | 156 | 3·3 | 0·097 | 15·13 | 6 |
| *Lepidoptera* | | | | | |
| 'Moths' | 14 | 0·3 | 0·187 | 2·6 | 1 |
| 'Butterflies' | 123 | 2·6 | 0·09 | 11·07 | 4·4 |
| Escapes | 163 | | | | |
| *Diptera* | 9 | 0·2 | 0·03 | 0·27 | 0·1 |
| Nematocera | 42 | 0·9 | 0·02 | 0·84 | 0·3 |
| Brachycera & Cyclorrhapha | 63 | 1·3 | 0·03 | 1·9 | 0·75 |
| *Hymenoptera* | 47 | 1 | 0·02 | 0·9 | 0·4 |
| 'Ants' | 227 | 4·8 | 0·002 | 0·45 | 0·2 |
| 'Wasps' | 120 | 2·5 | 0·02 | 0·24 | 0·1 |
| 'Bees' | 2910 | 62·3 | 0·015 | 43·65 | 17·4 |
| *Coleoptera* | 184 | 3·9 | 0·06 | 11·04 | 4·4 |
| Scarabaeoidea | 40 | 0·9 | 0·08 | 3·4 | 1·3 |
| Chrysomeloidea | 45 | 1 | 0·05 | 2·25 | 0·9 |
| *Other orders* | 9 | 0·2 | 0·16 | 1·5 | 0·6 |
| Unidentified | 51 | 1 | 0·015 | 0·77 | 0·3 |
| Other escapes | 105 | | | | |
| Totals | 4672 | 100 | | 250·24 | 100 |

No. of web-days 2809
Average daily catch 0·089 g

more than one per web per day. Of the other hymenoptera ants are the next most frequent class (227), they were almost entirely alates and their temporal distribution is very discontinuous. It is probably correlated with the occurrence of nuptial flights. Wasps totalled 120 and were almost entirely social wasps which nest in the buildings of the laboratory complex. Hymenoptera as a whole constitute 70·6% of the total catch (by numbers). Orthoptera constitute 11·4% of the total catch and (see later and Table 1) the greatest weight of insects caught. Tettigoniids totalled 306 and acridiids 219. Very few grillids were caught (eight). We recorded 269 captures of Coleoptera of which 45 were tentatively identified as chrysomeloids and 40 as scarabaeoids. We feel happier

Table 2. Monthly totals of insects caught by mature female *A. argentata* sample. Categories as in Table 1

| | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Odonata* | 16 | 4 | — | — | 1 | — | 2 | 4 | 3 | 6 | 4 | 8 | 48 |
| *Orthoptera* | | | | | | | | | | | | | |
| Grylloidea | 1 | 1 | — | — | — | — | — | 1 | — | 4 | — | 1 | 8 |
| Tettigonioidea | 61 | 26 | 2 | 17 | 33 | 29 | 26 | 18 | 15 | 23 | 33 | 23 | 306 |
| Acridoidea | 5 | 11 | 1 | 7 | 31 | 28 | 28 | 25 | 23 | 26 | 19 | 15 | 219 |
| Total | 67 | 38 | 3 | 24 | 64 | 57 | 54 | 44 | 38 | 53 | 52 | 39 | 537 |
| *Hemiptera* | 5 | — | 1 | — | 1 | 8 | 1 | — | — | 1 | 2 | 4 | 23 |
| Homoptera | 4 | 2 | — | 3 | 2 | 1 | — | 2 | 4 | 3 | 5 | 2 | 28 |
| Heteroptera | 13 | 6 | 4 | 3 | 21 | 29 | 11 | 9 | 12 | 18 | 17 | 13 | 156 |
| Total | 22 | 8 | 5 | 6 | 24 | 38 | 12 | 11 | 16 | 22 | 24 | 19 | 207 |
| *Lepidoptera* | | | | | | | | | | | | | |
| 'Moths' | 5 | — | — | — | — | 1 | — | 1 | — | 3 | 1 | 3 | 14 |
| 'Butterflies' | 17 | 3 | — | — | 9 | 14 | 16 | 17 | 14 | 15 | 11 | 7 | 123 |
| Total | 22 | 3 | | | 9 | 15 | 16 | 18 | 14 | 18 | 12 | 10 | 137 |
| *Diptera* | 2 | — | — | — | 2 | — | — | — | — | 3 | 2 | — | 9 |
| Nematocera | 1 | — | — | — | — | 2 | 3 | 6 | 12 | 15 | 2 | 1 | 42 |
| Brachycera & Cyclorrhapha | — | — | — | — | 2 | 14 | 13 | 11 | 5 | 11 | 1 | 6 | 63 |
| Total | 3 | | | | 4 | 16 | 16 | 17 | 17 | 29 | 5 | 7 | 114 |
| *Hymenoptera* | 4 | 11 | — | 2 | 4 | 11 | 2 | 1 | 4 | 1 | 5 | 2 | 47 |
| 'Ants' | 10 | 14 | — | 17 | 22 | 6 | 12 | 9 | 4 | 28 | 41 | 64 | 227 |
| 'Wasps' | 11 | 3 | — | 9 | 21 | 22 | 9 | — | 4 | 11 | 20 | 10 | 120 |
| 'Bees' | 318 | 161 | 75 | 21 | 367 | 343 | 342 | 167 | 287 | 423 | 174 | 232 | 2910 |
| Total | 343 | 189 | 75 | 49 | 414 | 382 | 365 | 177 | 299 | 463 | 240 | 308 | 3304 |
| *Coleoptera* | 8 | 19 | 2 | — | 26 | 13 | 13 | 33 | 28 | 25 | 11 | 6 | 184 |
| Scarabaeoidea | 3 | 2 | 8 | 1 | 3 | 7 | 1 | 1 | 1 | 3 | 6 | 4 | 40 |
| Chrysomeloidea | — | — | — | 9 | 14 | 4 | 8 | 1 | — | 1 | 4 | 4 | 45 |
| Total | 11 | 21 | 10 | 10 | 43 | 24 | 22 | 35 | 29 | 29 | 21 | 14 | 269 |
| *Other orders* | — | 2 | — | — | 1 | 2 | 1 | 1 | — | 1 | 1 | — | 9 |
| Unidentified | 1 | 4 | — | 5 | 8 | 8 | 3 | 2 | 2 | 2 | 10 | 6 | 51 |
| Totals | 485 | 269 | 93 | 94 | 568 | 542 | 491 | 309 | 414 | 623 | 369 | 411 | 4672 |

about the latter identification since we worked mainly on recognition by outline although we caught occasional glimpses of more diagnostic features such as antennal structure. The Hemiptera amounted to 4·4% of the total catch (207 individuals). Of these we were able to recognize 156 heteropterans (predominantly pentatomids) and 28 homopterans (mainly membracids). Lepidopterans amounted to 2·9% of the catch, with butterflies accounting for 123 records and moths for only 14. Lepidoptera escapes were recorded on 163 occasions. Thus, if our census is approaching accuracy, 54·3%

of the lepidopterans striking the webs escaped, despite the rapid restraint applied to this group of insects (see p. 345). The Diptera account for only 2·4% of the total catch. Of these 0·9% were Nematocera and 1·5% others which could not be identified to suborder but were not nematocerans. Since most of the nematocerans are digested in much less than two hours, our census may have underestimated the members of this group. (On the other hand, we find that very small flies strike the webs of *Argiope argentata* and are ignored by the spider; although they may be attacked by the theridiids which associate with the web.) Of the other insect orders only the Odonata account for more than 1% of the total catch (48 individuals amounting to 1·0% of the year's catch of insects). Insects of four other insect orders were positively identified. These were: alate termites (Isoptera), a mantid (Dictyoptera), a phasmid *Oncotophasma martini* (Phasmatodea) and several small neuropterans. Two arachnids were also caught (an *Argiope argentata* and an opilionid). Fifty-one prey packages contained insects which could not be identified at the ordinal level.

In terms of energetics, the numbers of prey caught may be far less important than the weight of prey. Although we did not remove prey from the web and weigh them, we can arrive at average weights for the various prey categories by weighing samples. We have done this and the results are set out in Table 1. We regard these estimated weights as conservative. Re-examining our data in terms of the weight of prey in each category, we find a dramatic shift in relative importance. Thus, the orthopterans become the most important prey, amounting to 55·2% of prey caught, and the hymenopterans drop into second place at 18·1% of the total weight. Odonata, Hemiptera and Lepidoptera all increase in relative importance when their weight is considered.

### *Seasonal variations in prey captures*

Our data permit the analysis of seasonal fluctuations in both the numbers and nature of prey. Tables 2 and 3, and Fig. 1 present three methods of analyzing the data on a seasonal basis. Table 2 shows the absolute number of insects of each category which the spiders caught in each calendar month of the study period. Table 3 shows the percentage of the total monthly catches which fall into each of our prey categories, and, in addition, the percentage of the yearly total represented by each monthly total. Figure 1 shows graphically the weekly catch of the five most frequently caught insect orders expressed as a percentage of the year's total catch for each of these orders. Also shown in this figure is a rainfall graph for the sampling period.

A number of interesting features of the seasonal pattern emerge from a consideration of these data. The dry season, January to mid-April, is a period which eventually becomes unfavourable to the *Argiope* population in the clearing at Barro Colorado Island. However, the driest month, January, is itself not a bad month in terms of prey captures since it accounts for 10·4% of the year's total catch and has the largest absolute number of Orthoptera captures (67). In the total number of prey caught it exceeds four wet season months: July, August, November and December. The fall in prey captures as the dry season progresses precedes the fall in the sample size of the spiders. February (with ten spiders throughout) has a total of 269 captures which is lower than any wet season month. The figures for March and April are low but during these months our sample fell below ten webs per day. The fall in prey captures in February suggests that the later reduction in spider population may be a consequence of a reduction in the numbers of available prey. This latter phenomenon does not occur immediately following the onset of dry conditions and is obviously a fairly complex response. In some cases insects may not be available to the spiders because of a behavioural change

Table 3. Prey captures by mature female *A. argentata* sample shown as percentages of each monthly total. Categories as in Tables 1 and 2

| | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Odonata* | 3·3 | 1·5 | — | — | 0·2 | — | 0·4 | 1·2 | 0·7 | 1·0 | 1·1 | 1·9 |
| *Orthoptera* | | | | | | | | | | | | |
| Grylloidea | 0·2 | 0·4 | — | — | — | — | — | 0·3 | — | 0·6 | — | 0·2 |
| Tettigonioidea | 12·6 | 9·7 | 2·1 | 18·1 | 5·8 | 5·3 | 5·3 | 5·8 | 3·6 | 3·7 | 8·9 | 5·6 |
| Acridoidea | 1·0 | 4·1 | 1·1 | 7·0 | 5·5 | 5·2 | 5·7 | 8·0 | 5·5 | 4·2 | 5·1 | 3·6 |
| Total | 13·8 | 14·2 | 3·2 | 25·1 | 11·3 | 10·5 | 11·0 | 14·1 | 9·1 | 8·5 | 14·0 | 9·4 |
| *Hemiptera* | 1·0 | — | 1·1 | — | 0·2 | 1·5 | 0·2 | — | — | 0·2 | 0·5 | 1·0 |
| Homoptera | 0·8 | 0·7 | — | 3·2 | 0·4 | 0·2 | — | 0·6 | 1·0 | 0·5 | 1·4 | 0·5 |
| Heteroptera | 2·7 | 2·2 | 4·3 | 3·2 | 3·7 | 5·3 | 2·2 | 2·9 | 2·9 | 2·9 | 4·6 | 3·2 |
| Total | 5·4 | 2·9 | 5·4 | 6·4 | 4·3 | 7·0 | 2·4 | 3·5 | 3·9 | 3·6 | 6·5 | 4·7 |
| *Lepidoptera* | | | | | | | | | | | | |
| 'Moths' | 1·0 | — | — | — | — | 0·2 | — | 0·3 | — | 0·5 | 0·3 | 0·7 |
| 'Butterflies' | 3·5 | 1·1 | — | — | 1·6 | 2·6 | 3·3 | 5·5 | 3·3 | 2·4 | 3·0 | 1·7 |
| Total | 4·5 | 1·1 | | | 1·6 | 2·8 | 3·3 | 5·8 | 3·3 | 2·9 | 3·3 | 2·4 |
| *Diptera* | 0·4 | — | — | — | 0·4 | — | — | — | — | 0·5 | 0·5 | — |
| Nematocera | 0·2 | — | — | — | — | 0·4 | 0·6 | 1·9 | 2·9 | 2·4 | 0·5 | 0·2 |
| Brachycera & Cyclorrhapha | — | — | — | — | 0·4 | 2·6 | 2·6 | 3·5 | 1·2 | 1·8 | 0·3 | 1·5 |
| Total | 0·6 | | | | 0·8 | 3·0 | 3·2 | 5·4 | 4·1 | 4·7 | 1·3 | 1·7 |
| *Hymenoptera* | 0·8 | 4·1 | — | 2·1 | 0·7 | 2·0 | 0·4 | 0·3 | 0·9 | 0·2 | 1·4 | 0·5 |
| 'Ants' | 2·0 | 5·2 | — | 18·1 | 3·9 | 1·1 | 2·4 | 2·9 | 1·0 | 4·5 | 11·1 | 15·6 |
| 'Wasps' | 2·2 | 1·1 | — | 9·5 | 3·7 | 4·1 | 1·8 | — | 1·0 | 1·8 | 5·4 | 2·4 |
| 'Bees' | 65·5 | 59·8 | 80·6 | 22·3 | 64·7 | 62·8 | 69·9 | 54·0 | 68·7 | 67·9 | 47·1 | 56·4 |
| Total | 70·5 | 70·2 | 80·6 | 52·0 | 73·0 | 70·0 | 74·5 | 57·2 | 71·6 | 74·4 | 65·0 | 74·9 |
| *Coleoptera* | 1·6 | 7·0 | 2·1 | — | 4·6 | 2·4 | 2·6 | 10·6 | 6·7 | 4·0 | 3·0 | 1·5 |
| Scarabaeoidea | 0·6 | 0·7 | 8·6 | 1·1 | 0·5 | 1·3 | 0·2 | 0·3 | 0·2 | 0·5 | 1·6 | 1·0 |
| Chrysomeloidea | — | — | — | 9·5 | 2·4 | 0·7 | 1·6 | 0·3 | — | 0·2 | 1·1 | 1·0 |
| Total | 2·2 | 7·7 | 10·7 | 10·6 | 7·5 | 4·4 | 4·4 | 11·2 | 6·9 | 4·7 | 5·7 | 3·5 |
| *Other orders* | — | 0·7 | — | — | 0·2 | 0·4 | 0·2 | 0·3 | — | 0·2 | 0·3 | — |
| Unidentified | 0·2 | 1·5 | — | 5·3 | 1·4 | 1·5 | 0·6 | 0·6 | 0·5 | 0·3 | 2·7 | 1·5 |
| Total as % of yearly total | 10·4 | 5·8 | 2·0 | 2·0 | 12·1 | 11·6 | 10·5 | 6·6 | 8·9 | 13·3 | 7·9 | 8·8 |

rather than a drop in their population. This may well be the case with some of the social hymenoptera, especially the *Trigona* which are so numerous in the prey capture records. Thus the period January–May is one during which a large number of entomophilous canopy trees are in bloom at the periphery of our study area. These flowers may constitute far richer food sources for *Trigona* than the flowers of the desiccating clearing. Thus, the bees may simply be attracted elsewhere. This view is supported by the fact that we found it difficult (and often impossible) to attract *Trigona* to syrup and fruit bait during these months, although worker activity at their nests was obviously high.

Until more is known about the seasonal ecology of the orthopterans, hemipterans and coleopterans in the vegetation type inhabited by our spiders, we cannot know what factors may operate to cause a fall in captures of these prey categories. It seems reasonable to assume that there will be reductions in the populations of phytophagous insects following the progressive desiccation of their food resources. Reduction in the degree of diurnal mobility in any or all of these groups would have a similar effect on prey captures and is not to be ruled out. The high catch of Odonata in January, twice that of any other month, could mean that the start of the dry season coincides with a peak in the adult dragonfly population. This itself could be a consequence of the drying up of ponds in which dragonfly nymphs develop.

A general reduction in insect availability during the dry season has been inferred by ornithologists working on Barro Colorado Island and elsewhere in lowland Panama. Some insectivorous birds switch from feeding on insects to feeding (at least partially) on fruit during this period (N. G. Smith, pers. comm.). A similar change in feeding habits occurs in some species of bats. Thus *Micronycterus hirsutus* supplements its basic diet of insects with a greater proportion of fruits during the dry season (Wilson, in prep.). The insectivorous bat *Myotis nigricans* stops breeding throughout most of the dry season and young born towards the end of this period are weaned at the onset of the wet season (D. E. Wilson, pers. comm.).

The coincidence of the onset of heavy rains and the resurgence of spiders, and in prey numbers, is very striking. May, the first month of the wet season, has a total of 568 prey captures which is exceeded only by October (623). It is the second highest month in terms of catches of Orthoptera, Hemiptera and Hymenoptera and the highest month for catches of Coleoptera. The fact that hemimetabolous insects return as important prey items suggests that development has started during the dry season or that the insects have aestivated through the dry season. A further possibility, that of immigration to the clearing from the surrounding forest cannot be ignored. The resurgence of the coleopterans may be accounted for by assuming that the rains trigger emergence from pupal stages (or that such emergence is synchronized with the onset of rain by the use of other cues).

There is another drop in total numbers in July when only 309 insects were caught. This drop is largely a consequence of a dramatic fall in the *Trigona* catch during July. These bees amount to only 54% of the month's total catch and 167 in absolute numbers (less than any other wet season month). November is another month with a low total catch and a low catch of Hymenoptera. Changes in the location of pollen and nectar sources may explain these two low sources.

Figure 1 shows that weekly variations in food caught by the spiders are very considerable, although, outside the dry season, only the dipterans and hemipterans ever reach a zero weekly score.

### *The average daily catch*

The average weight of prey caught by a spider, per web day, works out at 0·09 g wet weight (Table 1). On first consideration this seems a very low figure. Our figures for the difference between the wet weight of prey fed to *Argiope* and the weight of the remains dropped after feeding show a weight loss in the range 50–78% (varying from meal to meal and with the size and type of insect prey). If we assume that this weight loss is caused by ingestion of material from the prey during feeding, and take, arbitrarily, 75% as the proportion of the initial wet weight absorbed, we arrive at a figure of 0·068 g intake per spider per day. If we then assume that insect wet weights are made up of 60% water, then the dry weight intake becomes 0·02 g/spider day. In terms of calories, assuming 5000 cal/g dry weight of insect (a reasonable approximation, see Southwood, 1966; 360), this amounts to 100 cal/day. This figure does not take into account assimilation efficiency. Phillipson (1960*a, b*) gives an assimilation/consumption figure of 46% for the opilionid *Mitopus morio* (at 0·05 g body weight). If *Argiope argentata* achieves anything like this efficiency, the daily calorific intake may be around 40, for mature females. MacFadyen (1963) gives a metabolism figure of 27 cal/g for Araneae.

In order to determine whether *Argiope argentata* females could survive and lay eggs on a diet similar to that involved in our figure for the average daily catch, we fed five captive spiders on 0·06 g (wet weight) of food daily. The spiders, all mature females, were weighed at the start of the experiment and weighed at weekly intervals for a period of six weeks. We recorded the number and wet weight of the egg cocoons produced by each spider. The results are shown in Table 4. The weight of the individual

Table 4. Results of experimental feeding of captive female *A. argentata* on weighed quantities of domestic crickets. All weights are wet weights

| | Week I | | Week II | | Week III | | Week IV | | Week V | | Week VI | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Food: 0·06 g daily 0·422 g weekly | | | | | | | | | | | |
| Spider initial wt | Wt | Eggs | Wt | Eggs | Wt | Eggs | Wt | Eggs | Wt | Eggs | Wt | Eggs |
| A (0·455) | 0·458 | 0·21 | 0·56 | — | 0·52 | 0·076 | 0·55 | — | 0·52 | 0·023 | 0·41 | 0·23 |
| B (0·53) | 0·613 | — | 0·53 | 0·19 | 0·44 | 0·19 | 0·39 | 0·18 | 0·49 | — | 0·41 | 0·16 |
| C (0·625) | 0·784 | — | 0·64 | 0·27 | 0·76 | — | 0·61 | 0·23 | 0·75 | — | 0·642 | 0·09 |
| D (0·52) | 0·42 | 0·23 | 0·34 | 0·14 | 0·48 | — | 0·4 | 0·15 | 0·324 | 0·15 | 0·412 | — |
| E (0·379) | 0·376 | 0·17 | 0·504 | — | 0·47 | 0·18 | 0·41 | 0·2 | 0·53 | — | 0·493 | 0·18 |

spiders fluctuated up and down during the period, dropping after the production of eggs, but all the individuals produced at least three egg masses during the experimental period. Since we did not know the age of our experimental subjects or the date when they had mated—two factors which presumably affect growth and reproduction, the results strongly suggest that the diet was adequate for the maintenance of adult biological activities.

## DISCUSSION

Turnbull (1960) has given details of the types and numbers of prey caught by field populations of *Linyphia triangularis* Clerck, in England. He concluded that this species is a truly polyphagous predator, feeding at some time or another on all the insects which are available to it. The question of 'availability' with reference to the prey of orb web spiders is a most interesting one. Turnbull (1960) discusses the factors which will predispose any species to be caught in *Linyphia triangularis* webs. In summary, these are:

(1) Mobility, sessile or sedentary species are unlikely to approach or enter a web.
(2) Mobility in the appropriate zone of the habitat, species which are habitually confined, in their movements, to regions above or below the webs are unlikely to be trapped. Since the zone of the spider's web is essentially aerial, insects walking along vegetation are also unlikely to be trapped.
(3) Inability to react to the presence of webs, some species may avoid ensnarement because they can detect the presence of webs *and* are capable of making avoidance manoeuvres.
(4) Size and strength commensurate with web structure, small species may regularly pass through the web mesh whilst strong species may easily destroy the web and escape.

The first three factors would seem to apply to the prey of all the spiders which build snares of any kind. The fourth factor will equally apply to all orb weavers but will be strongly affected by the spider's specific web structure. Here there is not necessarily a simple correlation between spider size and mesh size or web strength. Some very large spiders may build large close meshed webs (e.g. *Nephila clavipes*) whilst others may build smaller, wide meshed, webs (e.g. *Argiope argentata*).

Our results, in general, support these basic assumptions. The insects which *Argiope argentata* caught regularly were either capable of flight or were strong jumpers. No lepidopteran larvae were caught despite their presence, often in large numbers, in the vegetation around the webs. Similarly, the regular catches of pentatomids were entirely of the winged adults. This despite the fact that nymphs were frequently very abundant on the *Pothomorphe* plants of the clearing. Leaf hoppers abound in sweep net samples from the study area but are almost absent in the prey records. This may be because their small size permits them to pass through *Argiope argentata* webs. There is good experimental evidence that insects as large as *Trigona* can pass through the webs in around 15% of cases (Robinson, Mirick & Turner, 1970). Almost the entire butterfly catch was made up of two species, *Anartia fatima* Fabricius and *A. jatrophae* (L.). These species are those which oviposit in low herbs and mate on vegetation close to the ground. Papilionids are numerous over the clearing area but seldom fly through the part of the clearing vegetation occupied by the spiders, they were seldom caught. The high number of lepidopteran escapes we recorded is striking confirmation of the escape potentialities of this group (see Eisner *et al.*, 1964). The number of other escapes, presumably from all the other prey groups, is less than that from the Lepidoptera alone. We are unable to comment on web avoidance other than to say that the highly manoeuvrable, and visually oriented dragonflies are caught fairly frequently. We have also seen a humming-bird caught in an *Argiope* web in the study area. (On this occasion, the spider fled the web, which held the bird for over three minutes before it eventually struggled free. We suspect that humming-birds may be predators of *Argiope argentata* since they certainly attack other orb weavers in the area.)

Kajak's (1965*a*,*b*, 1967) beautiful studies of the relationships between temperate grassland spiders and their prey are of great interest. Sampling the population of potential prey species presumptively available to the spiders (by sweep-netting and the use of sticky traps) she showed that there were very considerable differences between the potentially available and the prey actually caught. The explanation of these differences awaits, in the main, further detailed analysis. One explanation for gross differences between sticky trap yields and those of webs may lie in the penetrability of webs. Since the spiders which Kajak studied catch large numbers of small prey (90% were in the range 0·05–0·1 mg in 1965 data) we presume that her web samples included large numbers of immature spiders with close meshed webs. We predict that a comparison of prey caught by mature *Argiope argentata* and sticky trap data would yield exaggerated disparities because of the wide mesh size of the *Argiope* web. The problem of devising a system of sampling the prey which is actually available to mature large spiders has, we feel, not yet been solved. The sticky trap, in addition to catching prey which may pass through the adult web, may not hold large prey of the type which our spiders caught. It may further suffer from the great disadvantage of being much more conspicuous than an *Argiope argentata* web and, therefore, being avoided by larger, strong, flying prey. Sweep netting seems equally unsatisfactory since, apart from the fact that it acts selectively and frightens part of the fauna (Łuczak, 1958), it gives no indication of the activities of the insects which might bring them into the web region. These may vary daily and seasonally in such a way that prey species become available to spiders in a manner which may not be correlated with population size. These two sampling techniques may, therefore, provide data which are only of limited value for biological studies of large spiders which produce large meshed webs. We are presently carrying out a pilot study to determine the feasibility and utility of sampling web-capture-predisposing insect activity by observation (in collaboration with W. Graney).

Studies of the prey captured by tropical orb weavers may be of value in approaching the overall problem of seasonality in tropical environments and may, in addition, provoke a series of interesting questions about insect ecology in these regions. Our study of the prey of *Argiope argentata* arose from a restricted interest in the predatory behaviour of this species. A more comprehensive study could be designed to solve problems of greater generality and would be of great interest if it were carried out with forest spiders.

## SUMMARY

The prey caught by mature female *Argiope argentata* was censused over a period of one year. Ten webs (when available) were examined five times each day, at two-hourly intervals, between 09.00 and 17.00 hours. The prey animals seen in the webs were classified into orders and lower taxa, where possible. Escapes were scored and Lepidoptera escapes were separated from those of other prey by the characteristic presence of wing scales around the damage seen in the web. A total of 4672 prey was recorded for 2809 web days.

By numbers, hymenopterans (principally stingless bees) constituted the largest group of prey. Orthopterans were the second largest group. More lepidopterans escaped than were captured by the spiders and the number of such escapes exceeds that of all other escapes.

By weight, estimated by sampling, orthopterans were the most important group of prey and hymenopterans the second most important.

Prey captures fell off after the onset of the dry season. The fall in numbers of prey caught was followed by a drop in the spider population of the study area. The onset of the wet season coincided with an increase in prey numbers. Other fluctuations in the numbers and nature of the spider's prey are noted. It is suggested that a number of factors may be responsible for fluctuations in prey captures and that such fluctuations are not all necessarily correlated with fluctuations in insect population numbers.

The average weight of prey caught, per spider, per day, is estimated at 0·08 g. In captivity, a diet of around 0·06 g/day proved adequate for the maintenance of a high level of reproductive activity.

Factors which may predispose insects to be captured by orb web spiders are discussed in relation to the records of prey captures. Methods of sampling prey availability are discussed and it is suggested that, at present, there is no entirely satisfactory method of sampling this phenomenon.

It is suggested that studies of the prey caught by orb web spiders may be of value in approaching the problem of seasonality in tropical regions.

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## EXPLANATION OF PLATE

### Plate 1

Photograph of part of the study area showing typical wet season vegetational structure. A numbered marker indicates the position of an *Argiope argentata* web of the sample population.



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