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Rates of Egg Production by Tropical Spiders in the Field

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ABSTRACT

A simple technique, which involves hatching successive clutches of eggs found associated with individual spiders, gives measurements of rates of egg production from which rates of prey capture can be calculated in field populations. Assumptions involved in the technique are discussed. Calculated rates of egg synthesis in 12 field populations of six species of tropical spiders are presented. Despite their widely varying habitats of origin, all five small species produced about 5-10 percent of their body weight in eggs daily; the one medium-sized species produced about 3 percent daily. Conservative calculations of prey capture from egg production rates suggest that the small spiders captured 20-40 percent of their own weight daily, while the medium-sized species captured just over 10 percent. Intraspecific variation was high in the rates of egg synthesis; moderate in female weight, clutch size, and interval between clutches; and low in egg weight and female leg size. There was no tendency for later clutches to be smaller. Possible reasons for some of these patterns are given.

RESUMEN

Una técnica sencilla, en la cual se utilizan los datos obtenidos de la crianza de los contenidos de las múltiples bolsas de huevos encontradas con las hembras de ciertas arañas, da medidas de las tasas de producción de huevos en poblaciones en el campo. De estas tasas se pueden calcular tasas de captura de presas, y así estimar el impacto de las arañas sobre las comunidades donde viven. Se discuten algunas de las suposiciones de las cuales la técnica depende. Se presentan tasas de síntesis de huevos medidas en 12 poblaciones de 6 especies de arañas tropicales. A pesar de las grandes diferencias entre sus hábitats de origen, todas las cinco especies pequeñas sintetizaron diariamente una cantidad de huevos equivalente a aproximadamente el 5-10% del peso de su cuerpo; la especie de tamaño mediano produjo alrededor del 3% cada día. Cálculos conservadores basados en estos datos sugieren que las arañas pequeñas promediaron una captura diaria equivalente al 20-40% del peso de su cuerpo, mientras que la de tamaño mediano capturó un poco más del 10%. La variación intraespecífica en cuanto a la tasa de síntesis de huevos fue muy alta; fue moderada en cuanto al peso de las hembras adultas, el número de huevos/bolsa, y el intervalo entre desovadas; y fue relativamente baja en cuanto al peso de los huevos individuales y el tamaño (largo de la tibia primera) de las hembras adultas. Las arañas mayores de una especie dada tendían a poner más huevos por bolsa, y a producir huevos más rápidamente. No hubo tendencia clara a poner menos huevos en las últimas bolsas, dándose así una contradicción con los resultados de varios estudios de otras especies en cautiverio. Se proponen explicaciones posibles para algunos de estos patrones.

ONE OF THE KEYS to understanding how a given community functions is a knowledge of the rates of capture of materials or energy by the various component species. Precise measurements of rates of energy flow in the field are often difficult, especially for predators (e.g., Andrzejewska *et al.* 1967). This paper presents a simple technique used to estimate food intake rates based on egg production rates in several species of web-building spiders in natural habitats in Colombia and Panamá. These rates are compared with previous studies which utilized different techniques. Finally, correlations of relative reproductive effort with age, and of clutch size with spider size, are discussed, along with patterns in the variation of several parameters associated with egg production.

Three of the genera of this study, *Cyclosa*, *Dolichognatha*, and *Mecynogea*, are in the family Ar-

aneidae, and the fourth, *Synotaxus*, is in the family Theridiidae. None are particularly closely related, and their webs vary widely. *Cyclosa* build more or less vertical orb webs (fig. 1), *Dolichognatha* make nearly horizontal orbs, *Mecynogea* makes a closely woven horizontal non-sticky sheet orb suspended in the midst of a tangle of threads (see Lubin 1973 for a detailed comparison of this type of web with typical orbs), and *Synotaxus* make delicate, vertical "rectangular orbs" built on Cartesian rather than polar coordinates (Eberhard 1977a). They share, however, the common characteristic that females periodically lay relatively small clutches of eggs and place the egg sac in or near their webs, accumulating up to five or more sacs in a given web (fig. 1). By weighing and counting the eggs in different sacs, and then noting the differences in hatching times of eggs in successive sacs associated with a given spider, one can determine the rate of egg production for that spider during the period of time immediately preceding its capture. Then, using the ef-

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efficiency with which spiders have been found to convert prey weight into spider weight in other studies, one can roughly translate the rate of egg production into the rate of prey capture during this same period.

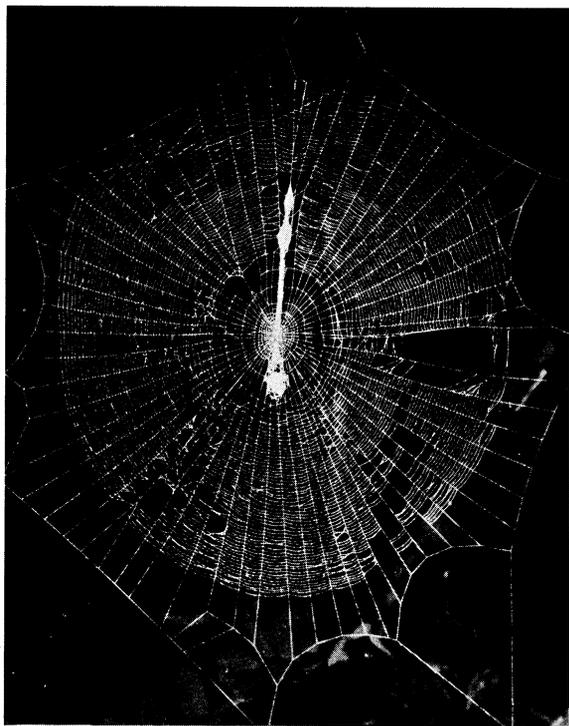


FIGURE 1. Orb web of *Cyclosa caroli* showing two egg sacs included in the web.

This technique depends on several assumptions. First, the rate of egg production must be directly proportional to the rate of prey capture. Other studies suggest that this is true. Turnbull (1962) showed that mature female *Linyphia triangularis* (Linyphiidae) in captivity used all the food they consumed for maintenance and egg production rather than growth, *i.e.*, their weight at death was nearly the same as that when they first molted to maturity. The data available suggest that araneid spiders have relatively uniform rates of metabolism (J. Anderson, pers. comm.). Riechert and Tracy (1975) found a linear correlation between the total weight of eggs produced by *Agelenopsis aperta* and the weight of food consumed from "subadult" stage until death. In addition, several studies (*e.g.*, Kajak 1967, Hagstrum 1970, Fujii 1972, Anderson 1974, Breymer and Józwick 1975, and Wise 1975) suggest that spiders in natural populations obtain suboptimal amounts of food.

Another possible drawback to the technique is

that mature spiders which have fewer than two egg sacs are necessarily excluded from analysis, since the technique depends on noting differences in hatching times for eggs in successive sacs built by the same spider. Spiders with higher egg-production rates might seem to be less likely to have fewer than two sacs than those with lower rates, and the calculated rates thus might overestimate the true rates. However, this factor is probably not important within the species studied, as is shown below.

It is also possible that the species of this study constitute a non-random sample with a bias toward high rates of egg production. In many spider species the female has only one egg sac with her at a time, and these species are not amenable to the type of analyses used here. These species might have only one sac due to lower rates of prey capture. The size of the clutch relative to the size of the female could also influence the likelihood that more than one sac would be found with a given female, since smaller clutches would be laid more frequently. The species of this study do have relatively small clutches when compared with other araneids (Eberhard, pers. obs.), and thus, tentatively, prey capture rates of the species of the study may not be far from typical rates for other araneids.

The technique has the limitation of not permitting the identification of prey. This may be partially offset by the fact that web-weaving spiders take a wide variety of prey (*e.g.*, Turnbull 1960, Robinson and Robinson 1970, 1973, Riechert and Tracy 1975). Direct measurements of prey "available" to web weavers involving sweep samples, sticky traps, and windowpane traps do not usually give realistic estimates for reasons discussed by Turnbull (1960) and Robinson and Robinson (1970).

There are three reasons that the technique probably underestimates true rates of prey capture. 1) Several laboratory studies have shown that the actual food intake of a variety of spiders fluctuates widely even when prey are supplied *ad limitum* (*e.g.*, Miyashita 1968, 1969, Haynes and Sasojevic 1966, Turnbull 1962, Peck and Whitcomb 1970); feeding is consistently reduced during the periods immediately preceding egg laying and molting. Feeding by *Nephila maculata* in the field also decreased just prior to oviposition (Robinson and Robinson 1973). The spiders of this study were all mature females, so molting would not influence the data, but oviposition might. The species of this study are somewhat unusual among spiders in producing relatively high numbers of clutches with relatively short delays between them (minima of one to three days in the

TABLE 1. Averages from 12 samples of six species of web-building spiders. The numbers in parentheses represent the numbers of individuals in the samples (in the case of egg weights, the numbers of clutches weighed), and the percentages represent the coefficients of variation (= standard deviation/mean). Assumptions made in the calculations are discussed in the text.

Spider	Site date	Weight of female (mg)	Tibia length	"Basic" female weight (mg)	Number of eggs per clutch	Weight of egg (mg)	Days between clutches	Eggs Produced/day	Weight of eggs (mg)/day	Daily egg production in terms of "basic" female weight (%)	Estimated daily capture in terms of "basic" female weight (%)	Density of spider population	Temperature at which eggs were raised as opposed to that of the natural environment
<i>Aranidae</i> <i>Cyclosa caroli</i>	B.C.I. VIII 74	16.0 21%	9.8%	14.23	36.6 (43) 31%	0.095 (17) 4.8%	2.6 (43) 35%	14.1 59%	1.34	9.4	38	dispersed	similar
	Rio Jamundi V 74	8.1 (11) 36%	12.5%	6.98	18.3 (22) 34%	0.12 (27) 11%	4.5 (22) 45%	4.1 50%	0.49	7.0	28	very dense	slightly higher
	Saladito	7.0 (31) 27%	5.2%	5.78	13.1 (35) 43%	0.18 (16) 12%	4.6 (35) 51%	2.8 54%	0.50	8.7	35	moderately dispersed	much higher
	Anchicaya V 74	3.2 (9) 21%	4.8%	2.72	9.5 (10) 29%	0.11 (15) 13%	4.6 (10) 37%	2.1 49%	0.23	8.5	34	very dispersed	slightly lower
<i>Dolichognatha</i> sp. #1	Lago Calima IX 73	6.7 (30) 33%	—	5.82	13.0 (63) 49%	0.13 13%	5.4 (63) 33%	2.4 64%	0.31	5.3	21	very dense	higher
	Rio Jamundi V 74	7.5 (19) 36%	11%	6.37	17.4 (45) 34%	0.13 (9) 10%	5.7 (45) 37%	3.1 57%	0.40	6.3	25	very dense	similar
	Rio Jamundi VI 75	5.6 (15) 24%	10%	4.63	14.6 (19) 46%	0.13 (11) 16%	5.6 (19) 38%	2.6 84%	0.34	7.3	29	very dense	similar
	Rio Pance IX 73	3.3 (18) 29%	5.8%	2.62	11.3 (26) 34%	0.12 (27) 16%	4.7 (29) 27%	2.4 64%	0.29	11.1	44	moderately dense	slightly higher
<i>Mecynogea lemniscata</i>	El Castillo IV 75	4.2 (22) 20%	8.9%	3.61	10.5 (40) 29%	0.12 (6) 8.9%	1.1 (40) 37%	1.7 57%	0.20	5.5	22	dispersed	similar
	Pan Am. Highway VIII 74	97.7 (9) 29%	—	90.5	27 (13) 42%	0.53 (9) 14%	6.3 (20) 34%	4.3 67%	2.28	2.5	10	moderately dense	similar
<i>Theridiidae</i> <i>Synotaxus turbinatus</i>	Washington, D.C. VIII 76	17.9 (11) ^a 35%	—	15.5	9.6 (15) 30%	0.40 (8) 9.9%	5.6 (15) 50%	2.0	0.80	4.5	18	moderately dense	slightly higher
	B.C.I. X 75	5.9 (11) 24%	—	4.9	19.2 (14) 32%	0.11 (14) 16%	4.9 (18) 39%	5.0	0.49	10.0	40	moderately dispersed	slightly lower

^aSomewhat underestimated, since spiders were not weighed until four days after capture.

different species). If they reduce their feeding rates prior to oviposition, the rates of prey capture calculated by the technique underestimate the true rates of prey capture by active spiders. 2) Spiders probably assimilate less of their prey which is captured soon after large meals (*e.g.*, Kajak's 1965 study of *Nuctenea cornutus* (= *Araneus cornutus*)). In general, assimilation rates are probably greater when the prey is small in relation to the spider (Turnbull 1962, Breymer and Odum 1969). Since the data on rates of conversion of prey weight to spider weight were obtained with moderate to small prey (see below), the use of these rates in this study may overestimate the rate of conversion of prey weight to spider weight. This would result in underestimates of prey capture rates based on egg-production rates. 3) The spiders of this study may have higher metabolism rates than the species for which the conversion of prey weight to spider weight has been measured. Web construction, which lasts 0.5-1 hour/day for all species except *M. lemniscata*, involves an approximately 50 percent increase in metabolic rate (Peakall and Witt 1976). Recycling web proteins involves another, relatively small metabolic loss (Peakall 1971), and it is possible that some species do not reingest their webs and thus suffer a greater loss (Barreto and Eberhard, in prep.). Egg synthesis also probably involves increased metabolic rates. Araneid spiders may also have unusually high standard rates of metabolism (Myrcha and Stejg-willo-Laundanska 1970, Peakall and Witt 1976, J. Anderson pers. comm.).

METHODS AND SITES

The data in table 1 were obtained in the following manner. Female spiders were collected with their egg sacs, and weighed to the nearest 0.1 mg within 24 hours of capture; the eggs from a random sample of sacs were also weighed in groups of at least five. The sacs associated with each female were opened individually, the eggs or spiderlings within counted, and each sac and its contents were kept separately in a cotton-stoppered glass vial which was rechecked at the same time daily. Three events were noted: hatching to first-stage post-embryo; molting to second stage post-embryo; and molting to second instar (terms of Peck and Whitcomb 1970). All three events normally occur within the egg sac in nature, and each one provided a reference point to compare the relative development of young in different sacs. The differences in development between sacs in which two or three different events could be com-

pared were thus measured somewhat more accurately than to the nearest day.

The temperature regimes of the eggs in vials were in some cases different from those in nature, and the estimated magnitudes of these differences are indicated in table 1. The most doubtful figures are those for *Cyclosa* sp.n. from Saladito; the developing eggs and nymphs of this species were kept at about 23°C, probably 5-10°C above the average temperature of the environment from which they came. There do not appear to be any studies of the effect of temperature on the development rates of spider eggs. Water was periodically dripped onto the cotton stoppers of the vials, but otherwise no attempt was made to control humidity.

In the *Cyclosa* species the numbers of eggs in sacs which second instar spiderlings had already deserted were also determined by counting the numbers of cast second-stage post-embryo skins, which had a mother-of-pearl sheen and were easily identified. This was not possible in *Dolichognatha* spp. because the second-stage post-embryos were active, apparently breaking down the walls between sacs and at least occasionally moving from one to another. Sizes of older clutches were easily determined in *Mecynogea* because the second instar spiderlings remained in their sacs and could be counted there.

To facilitate comparisons between species by eliminating the influence of species differences in the percentage of the female's weight dedicated to eggs, rates of egg synthesis were calculated in terms of the female's "basic" weight—the average weight of females not counting the eggs being synthesized for the next clutch. Since some of the females collected in the field had probably oviposited recently, others were swollen with eggs and about to oviposit, and others were in intermediate states, the "basic" weight was calculated by subtracting one half of the mean clutch weight from the mean female weight on the assumption that females were on the average halfway between clutches.

The sites² at which the spiders and the eggs were collected were all in Valle, Colombia (unless otherwise noted); the ecological zones of the Colombian sites are according to Espinal and Montenegro (1963).

²Anchicayá (el. 400m, on the road between Cali and Buenaventura—pluvial rain forest zone)—forest from which some trees have been removed but which is in a relatively natural state;

Barro Colorado Island, Canal Zone (el. about 30m—monsoon forest zone)—secondary forest in a relatively advanced stage of regeneration;

Finca El Castillo (el. 100m, on the floor of the Cauca Valley near the junction of Rio Jamundí and Rio Cauca

RESULTS AND DISCUSSION

RATES OF EGG SYNTHESIS

The data in table 1 show that the rates of egg synthesis, in terms of the percentage of the "basic" weight of the female, are similar for all the typical orb weavers and the "rectangular orb" weaver *Synotaxus* (5.3-11.1%/day). This similarity seems remarkable in view of the large differences in web design and habitat (temperature, spider density, rain, which probably greatly lowers an orb web's efficiency as a trap, and human modification).

The values for the sheet orb weaver *Mecynogea* were lower (2.5, 4.5%/day). This finding may support the idea of Lubin (1973) that the sheet type of web is a less effective prey trap, but the larger size of *M. lemniscata* may also be involved, and the smaller spiders (Washington, D.C.) had higher rates (see next section). Fragmentary unpublished data on *Cyrtophora moluccensis* (kindly supplied by Lubin), another large species which spins a web very similar to that of *Mecynogea*, give a similar low rate of egg synthesis—3.1%/day. These egg-synthesis rates are probably comparable to measurements of growth rates for non-captive araneids made by Kajak (1967), and have at least somewhat similar values: she measured daily growth/spider weight values for various instars of *Singa hamata* that varied between 1.5 and 6.9 percent (average 3.7%).

The idea that spiders with fewer egg sacs probably capture less prey, and that consequently the technique used to obtain the values in table 1 probably gives overestimates of true egg production rates, was tested by comparing the rates of egg production for spiders with two sacs containing eggs or young,

- dry tropical forest zone)—an approximately 1500-6000 m² patch of secondary or cut-over primary forest set in swampy pastureland (all spiders collected at least 20m from the edge of the pasture);
- Lago Calima (el. 1400m, near the road between Buga and Loboguerrero—very humid subtropical forest zone)—a dense, relatively old bamboo thicket about 20m in diameter in the midst of open pasture;
- Pan American Highway, Canal Zone (el. about 50m, between Araján, Panamá and Panamá City—monsoon forest zone)—brush growing between a grassy roadcut and forest;
- Rio Jamundí (el. 1000m, near road between Cali and Jamundí—dry tropical forest zone)—a bamboo thicket about 20m wide along one bank of a small river running through open pasture;
- Rio Pance (el. 1050m, near Cali—dry tropical forest zone)—along the edges of a small stream in a brushy cleared area;
- Saladito (el. 1800m, near the pass on the road between Cali and Dagua—humid low mountain forest zone)—forest from which some trees have been removed;
- Washington, D.C., U.S.A.—in bushes on the grounds of the National Zoo.

versus those of spiders with three inhabited sacs (table 2). Only the most recent clutch for each spider was used to assure that all clutches were made during more or less the same time period. The results show that there was no significant tendency for spiders with two inhabited sacs to produce eggs more slowly than those with three. Extrapolating, spiders with only one or no sacs probably also have similar egg-production rates, and it seems likely that the rates in table 1 are not overestimates on this account.

RATES OF PREY CAPTURE

The data for egg-production rates can be roughly translated into rates of prey capture by taking into account assimilation efficiency. Adult *Linyphia* females feeding on small prey converted 15-30 percent of the dry prey weight into dry spider weight (Turnbull 1962, fig. 5A; data for normal-sized females are in the upper portion of this range). Similar data for the lycosid *Tarantula* range between 21 and 33 percent (Hagstrum 1970, Table 6 for individuals weighing less than 16 mg), and the corresponding value for *Lycosa rabida* is 32 percent (Van Hook and Moulder 1969, in Hagstrum 1970). In all three cases approximately 25 percent of the prey weight is converted to increased spider weight. One can thus reason that a clutch of x mg probably required approximately $4x$ mg of prey. Given this assumption, calculations made on the egg-production rates of the true orb weavers and *Synotaxus* yield daily prey capture rates of 21-44 percent of the "basic" female

TABLE 2. Comparisons of egg production parameters between spiders with three egg sacs and those with two (data from 8 sites, 6 species in total); there was no clear tendency for spiders with two sacs to have lower values than those with three.

	Clutch size	Interval between last and next to last clutch	Rate of egg production
Species in which the average for spiders with two sacs was greater than for those with three	3	4	5
Species in which the average for spiders with two sacs was greater than for those with three	5	3	3
Species in which the averages were equal	0	1	0

weight (table 1) (or 19-35 percent of measured female weights), while those of *M. lemniscata* give 10-18 percent (9-15 percent of measured female weight).

COMPARISONS WITH OTHER STUDIES

There are several previous field studies involving rates of prey capture by spiders. The most satisfactory are those of Robinson and Robinson. In Panamá (1970) they checked a series of adult female *Argiope argentata* (Araneidae) (wet weight about 500 mg) and their webs every two hours during the day for a year, noting whether the spider was feeding, and if so, on what. They found that on the average each spider captured about 90 mg, or about 18 percent of its body weight daily. In New Guinea (1973), they studied the predatory activity of *Nephila maculata* (Araneidae) (wet weight about 3000 mg) by daily collecting the discarded remnants of the spider's prey from beneath their webs, and identifying them, and then estimating their wet weight from freshly killed specimens of the same species. They obtained remains of about 618 gms of prey in 3237 spider days, giving a daily rate of 190 mg/spider or about 6 percent of its weight. Eberhard (1977b) used a similar technique to estimate that the adult female bolas spider *Mastophora* sp. (Araneidae) (weight about 750 mg) captured about 18 percent of its body weight/night of hunting. Taking into account the nights prior to ovipositions when the spiders did not hunt, the rate is reduced to about 14 percent.

Other less tedious methods have not been as satisfactory. Wise (1975) checked webs of *Linyphia marginalis* (Linyphiidae) (web design similar to that of *M. lemniscata*, but spider weight only about 11 mg) frequently during three- to four-hour periods and noted "fruit fly equivalents" of prey seen being consumed. Assuming a fruit fly wet weight of 0.6 mg, the 80 "fruit fly equivalents" he saw in 41 days gives $1.95 \times 0.6 = 1.2$ mg captured/day, or about 11 percent of the spider's weight. The data were all taken during the day, however (Wise pers. comm.), and since densities of flying insects often vary greatly at different hours of the day (e.g., Taylor 1958, Hespeneide 1975), they must be treated with caution.

Riechert and Tracy (1975) counted captures in sticky model webs and multiplied these by average attack efficiencies of the sheet web spider *Agelenopsis aperta* (Agelenidae) (wet weight about 500 mg) to obtain estimates of prey consumption which ranged from about 22 to 3 percent of the spider's weight

at different sites. It is difficult to assess their results. Their model webs lacked an important part of at least some *Agelenopsis aperta* webs, the upper barrier mesh which presumably acts to knock flying insects down onto the sheet below. The sight of the traps was undoubtedly different from that of real webs, and may have affected the tendency of prey species to land there. The average attack efficiency, given as 60 percent, is also probably strongly influenced by the species used as prey (unspecified).

Breymeyer (1967) and Breymeyer and Józwick (1975) estimated from periodic collections of lycosids in the field that the spiders captured between 3 and 12 percent of their weight daily.

Kajak (1965, 1967) attempted to determine predation rates by inspecting webs of *Nuctenea cornutus*, *Araneus quadratus*, and *Singa hamata* (all Araneidae) during the day (apparently the spiders were not on the webs but hiding off them; in the eastern United States *N. cornutus* rebuilds its web in the evening and sits on it only at night) and counting the numbers of prey caught in them. This method seems inadequate since these spiders are probably most active at night, so daytime prey are not really available to them. More importantly, many or most prey are only momentarily detained in orb webs, but are captured due to the spider's active attack behavior (e.g., Barrows 1915, Robinson *et al.* 1969), and these prey would not be counted with Kajak's technique. Van Hook (1971) also studied energy flow in *Lycosa* spp. (Lycosidae) populations, but neglected to attempt field measurements on the rates of prey capture.

On the whole, the predatory rates calculated in this study are higher than those obtained in other studies. The species of this study are approximately two orders of magnitude smaller than most of the others (including those of the most reliable studies), and their food requirements may be higher on a per weight basis (e.g., Breymeyer and Józwick 1975). As shown in figure 2, the available data for araneids appear to correlate well with the weight of the spider.

COMPARISONS OF VARIATION

The amount of variation in some of the measurements in table 1 (indicated by the coefficients of variation for each sample) appeared to fluctuate systematically. The most widely variable factor was the number of eggs made per day (av. coeff. of var. 61 percent, range 49-84 percent). This figure undoubtedly reflects the chancy nature of most orb weavers' lives. Prey probably arrive more or less randomly at the web and, in addition, unfortunate

events, such as a leaf or a twig falling and breaking the web, rain falling soon after a web is built, or a large animal's blundering through it, are largely beyond the spider's control. The fact that *M. lemniscata* did not have less variation despite having a much more durable web argues that the irregular arrival of prey was the most important factor.

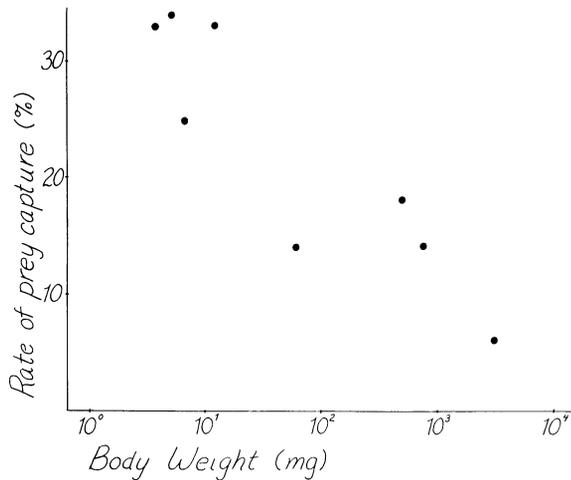


FIGURE 2. Apparent relationship between species body weight and rate of prey capture expressed in terms of percent of body weight captured daily: smaller spiders seem to capture prey faster. The data for the three heaviest species are from other studies (Robinson and Robinson 1970, 1973, Eberhard 1977b) in which other techniques were used. Although the data show a statistically significant relationship, the trend must still be considered tentative.

Other variables such as female weight, number of eggs per clutch, and the number of days between clutches varied less ($p < 0.01$), all having average coefficients of variation between 20 and 51 percent (av. 34 percent). These variables, while similarly influenced by chance events, are probably also partially determined genetically. The variation of female weight in these species may be unusually low for spiders since they produce relatively small clutches in terms of their body weights (Eberhard, unpub.), with the result that the weight gained and lost by females during a cycle of feeding until oviposition is probably relatively small.

Data permitting calculation of coefficients of variation for clutch sizes of other species of spider in the field have been published for five families: 39, 23, and 21 percent for three species of Araneidae (Coyle 1971); 36 percent for one species of Dugesiidae (Bentzen 1973); 23 percent for one species of Theridiidae (Tanaka 1973); 22 percent for one species of Micryphantidae (Tanaka 1973);

and 15, 13, 17, 18, 18, 19, and 29 percent for eight species of Lycosidae (Kessler 1973, data for the year 1968). The lycosid clutches show significantly less variation than those of this study ($p < 0.01$), while the others are not significantly different. The lycosids lay only one or sometimes two clutches (Kessler 1973) while the others, like the species of this study, typically lay long series of sacs (the antrodiaetids over several years), and this difference may be responsible for the lower lycosid variation since their oviposition might well be less opportunistic.

Two further variables, egg weight and tibia length, showed even less variation (av. coeff. of var. 10 percent, range 4.8-16 percent) ($p < 0.01$) compared with the two groups of variables above, indicating that unforeseen short-term local environmental variations had relatively little influence on egg and spider size. Studies of other spiders have also demonstrated small variation in egg weights (Kessler 1971, 1973; Wise 1975), although a study of laboratory-raised *Linyphia triangularis* showed large variations in egg weights combined with small variations in clutch size (Turnbull 1962), and semi-captive *Agelenopsis aperta* responded to high feeding schedules by increasing egg size (Riechert and Tracy 1975).

OTHER RELATIONSHIPS

There was a large difference in spider size between sites for both *Cyclosa* species and for *M. lemniscata*. In all three species, the larger spiders laid more eggs per clutch ($p < 0.01$ for *C. caroli* and *M. lemniscata*, $0.1 > p > 0.05$ for *C. sp. n.*). In *C. sp. n.* and *M. lemniscata* the larger form's eggs were larger, but in *C. caroli* they were smaller (all $p < 0.01$). In one species (*Dolichognatha* sp. #1) there was also a positive correlation between spider size (tibia length) and clutch size ($p < 0.05$, $N = 34$), and there were similar insignificant tendencies in the other species. Larger body sizes of individuals of a given species are at least partly due to better juvenile feeding (e.g., Turnbull 1962), and in all species the larger forms produced egg material faster, although their rates per body weight were nearly equal. Positive correlations between spider and clutch size have been documented in several lycosid species (Peterson 1950, Kessler 1973), and in *Linyphia marginata* (Wise 1975), but were lacking in a laboratory study of *L. triangularis* (Turnbull 1962). The reason why the large *C. caroli* form produced relatively small eggs is not clear.

Although one might expect that, within a given species, clutches with more than the median number

of eggs would be preceded by longer than median delays (*i.e.*, would take longer to synthesize), just the opposite seemed to be the case. In two species (*C. caroli* from Barro Colorado Island and *Dolichognatha* sp. #1), when the clutches above and below the median were compared as to whether they were preceded by longer or shorter delays (in relation to the median delay), larger clutches were made in less than the median delay, and vice versa ($p < 0.01$ for both species). The other species showed similar but insignificant tendencies.

In several spider species it has been noted that in captivity the number of eggs in successive clutches gradually decreases (*e.g.*, Buche 1966, Mikulska and Jacunski 1968, Kessler 1971, Kullmann 1961, Peck and Whitcomb 1970, Taylor and Peck 1974, Valerio 1976). This tendency is in accord with theoretical expectations for species with high adult mortality rates (*e.g.*, Williams 1966). However, when the numbers of eggs in successive clutches of the species of this study were compared, each clutch with the one immediately preceding it, there was no significant tendency for later clutches to have fewer eggs in any species. When the newest (latest) clutches in series of three or more sacs were compared with the oldest, the newest were significantly smaller in only one species (*Dolichognatha* sp. #1), and there

was no significant difference when the data for all species were combined. The field data for these species thus fail to support conclusively laboratory observations. Bentzien (1973) also failed to find significant tendencies in a small sample of *Diguetia imperiosa* (Diguetidae) egg sacs from the field, but Kessler (1973) did find significant decreases in the sizes of later clutches of four lycosid species in the field. It is conceivable that short-term fluctuations in prey abundance and capture success masked tendencies to change clutch sizes; and, as noted above, lycosid clutch size may be less responsive to environmental variations. It is also possible that sperm reserves affect clutch size (M. Robinson, pers. comm.), and that the spiders in captivity, without access to males, produce successively smaller clutches as they use up the sperm in their spermathecae.

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