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ENVIRONMENT, REPRODUCTION AND THE SEX RATIO OF THE SOCIAL SPIDER *ANELOSIMUS EXIMIUS* (ARANEAE, THERIDIIDAE)[1]

Fritz Vollrath

Smithsonian Tropical Research Institute
Balboa, Republic of Panama[2]

ABSTRACT

Three populations of the neotropical theridiid *Anelosimus eximius* were studied, one in the lowlands were the year shows distinct seasonal cycles, a second in the intermediate uplands, and a third in the mountains where seasonal changes in climate are less pronounced. Colonies in the lowlands showed a large monthly variation in egg production, presence of immature spiderlings and colony biomass. Colonies in the mountains showed less variation. In all sites the sex ratios were variable but were always skewed in favor of females. The sex ratio bias was independent of seasonal factors. It was presumably also independent of other environmental factors, with the exception of predation, which apparently was suffered more by females.

INTRODUCTION

Even in the tropics, seasonal change in the environment has an observable influence on the presence of many short lived organisms. In tropical Panama many terrestrial invertebrates like insects (Wolda 1977, 1978) and spiders (Robinson and Robinson 1970, Lubin 1978, 1980) show clear annual cycles or seasonal depressions in activity and/or abundance. Towards the end of the dry season, for example, very few spiders are present in the lowlands whereas they are quite abundant at most other times of the year. Colonies of the social spider *Anelosimus eximius,* however, persist for many years at the same location and are active in the dry season when most other spiders have vanished.

The effects of the environment on *A. eximius* were studied by comparing colonies in several sites with different degrees of seasonal change. Colonies generally raise about two generations a year and special interest was taken in the reproductive aspect of a colony's cycle, including egg production and the ratio of the sexes. Like in other social spiders (Buskirk 1981) but unlike the solitary spiders (in Lit.), the sex ratio of *A. eximius* is heavily skewed in favor of females (Christenson 1984, Vollrath 1985, Aviles in press).

Anelosimus eximius (Keyserling) is a neotropical social theridiid (Levi 1956, 1972). Many individuals share a communal web (nest, colony) and cooperate in web-building and prey capture (Simon 1891, Brach 1975, Tapia and DeVries 1980, Vollrath 1982, Christenson 1984). Colonies forming part of a cluster are

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[2] Mailing address: Department of Zoology, South Parks Road, University of Oxford, Oxford, OX1 3PS, UK.

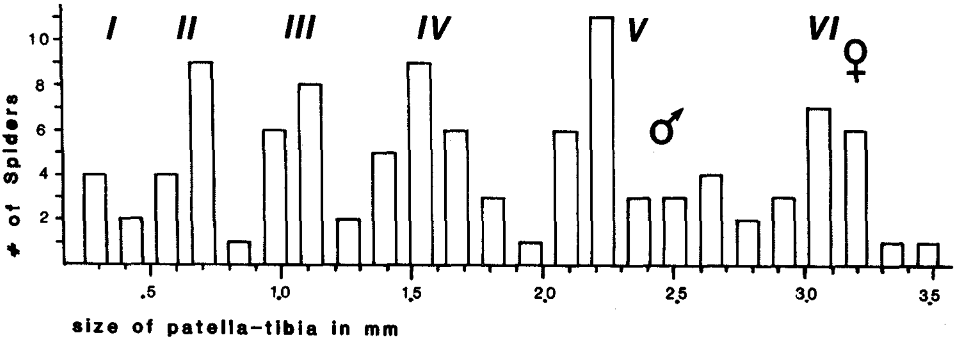

Fig. 1.—Histogram displaying the size distribution of *Anelosimus eximius* collected in two colonies in Panama. The length of the patella-tibia of the first leg was measured. Mature males were found in size 2.4 mm, mature females from size 3 mm upwards. The roman numerals above the columns indicate the instars (beginning with I at eclosion from the egg sac).

founded by budding, or by one female which may be joined by others (Christenson 1984), all having been inseminated in the parental nest (Vollrath 1982). Colonies far from other colonies are presumably founded by single females since emigrant females seem to travel alone (Vollrath 1982). A well established colony can grow to contain many thousand individuals in one nest, and a colony cluster with its offshoot nests may persist for many years in one site (Robinson pers. comm., Vollrath unpubl.). However, few single female foundations are successful and colony clusters are few and far between (Vollrath 1982, Christenson 1984).

Adult males are smaller and weigh less than adult females (Levi 1963). It appears that after emergence from the egg case the male undergoes four molts to reach maturity, whereas the females mature in the fifth or sixth instar (Fig. 1). Both sexes reach maturity about two months following eclosion, (Aviles in press) although growth can be slightly faster or considerably slower (Overal and Ferreira 1982). In the field adult females have been observed to live for approximately three months (Aviles in press), and under laboratory conditions they may live up to 4 months, males lived up to two months in the lab (Vollrath unpubl.).

The egg cases are spheres 4 mm in diameter, covered with tough grey silk and containing from 17 to 53 eggs, depending on the locality and the nutritional state of the colony (Vollrath unpubl.). The spiderlings are ready to leave the egg case after about 20 to 30 days (Overal and Ferreira 1982, Aviles in press). They emerge readily when the average relative humidity is high, but when it is low they stay inside the protective egg case and may even die there. Egg sacs are constructed in the center of the colony and are tended (guarded) there by subadult or adult females. Tending entails carrying the egg sac in the chelicerae and manipulating it with the mouth parts (Christenson 1984). It is possible that the spiderlings cannot open the egg sac by themselves, and need a female's help. Egg sacs may be cannibalized—opened by members of the colony and the contents eaten (Christenson 1984).

All members of the colony from instar three onward (with the notable exception of the adult males) contribute towards colony maintenance, web construction and repair, and prey capture (Tapia and DeVries 1980, Christenson 1984). Like most male spiders, males of *A. eximius* leave a dragline behind when moving about but they do not appear to do so in the orderly fashion of an immature or a female *Anelosimus* repairing the nest or the capture threads. Male prey only on small insects which they do not share. Males do, however, join female feeding aggregations. Spiderlings of the first instar may feed on prey captured and predigested by older instars. More often they are seen soliciting and receiving regurgitation fluid from females (compare Kullmann and Kloft 1968, Lubin 1982).

In Panama, *A. eximius* is found at forest edges or inside the forest, in clearings or tree falls, where the webs are built at heights between 1 to 6 meters. The communal web consists of a horizontal, tightly woven bowl (the retainer web) with a loose network of vertical threads (the snare) above. Flying or jumping insects are arrested in their path by the vertical threads and tumble onto the retainer web, where they are chased by the spiders. The bowl section of the web consists of many layers of silken threads, laid down continuously during the entire life of the nest. It is remarkably strong, comparable to a fine fabric. Holes ripped by falling twigs or cut by foraging ants are quickly repaired. In the dry season, the spiders are less active, and leaves accumulate in the web changing the appearance of the colony (compare Fig. 2 in Simon 1891; Fig. 1 in Brach 1975; Fig. 1 in Vollrath 1982; Fig. 1 in Christenson 1984).

The numbers of spiders in a colony (colony size) is correlated with the size of the bowl webbing (Fig. 2), which enabled me to estimate the spider population of colony clusters from the size of individual webs. The estimate for one colony complex in El Valle was about 40,000 spiders in 37 colonies (nests), stretching 30 meters along the edge of a small forest. The estimated mean colony size was 1130 spiders (± sd 1150).

In the same habitat, and often adjacent to colonies of *A. eximius,* one may find single nests of the subsocial congeneric *Anelosimus juncundus* (O. P.-Cambridge). On rare occasions, as observed in the El Valle highlands, the small individual webs of single *A. juncundus* females were joined by a dense network of threads, thus forming large webs containing several mature females and their offspring. These webs correspond in their dimensions to colonies of *A. eximius* (Fig. 2) and closely resemble nests of this species. Adult females in aggregations of *A. juncundus* are highly aggressive towards one another and spread themselves out inside the shared web structure. The immatures, in contrast, mingle freely. In *A. eximius* individuals of all stages seem to be attracted to one another, during the day they form dense aggregations of spiders in the retreats.

MATERIALS AND METHODS

The data presented here were collected during a study of *A. eximius* in Panama (April 1978-May 1979), where three sites were studied in detail: (a) the lowland semi-decidous forest (altitude 30 meters above sea level) on the Bohio Peninsula (79°49′, 9°11′) and the Pipeline Road Site (Parque Nacional Soberania 79°45′, 9°10′), (b) a similar site at a higher elevation (300 meters) at the El Llano-Carti Road (79°4′, 9°15′), and (c) two locations in the cloud forest near El Valle (elevation 880 meters, 80°9′, 8°37′). Colonies were also collected from Anchiote Road (80°, 9°29′), Mahe-Bayano (78°49′, 9°81′) and El Cope (80°27′, 8°38′).

The climate in lowland Panama has two distinct seasons: a rainy season from May to December and a dry season from January to April. Although neither air

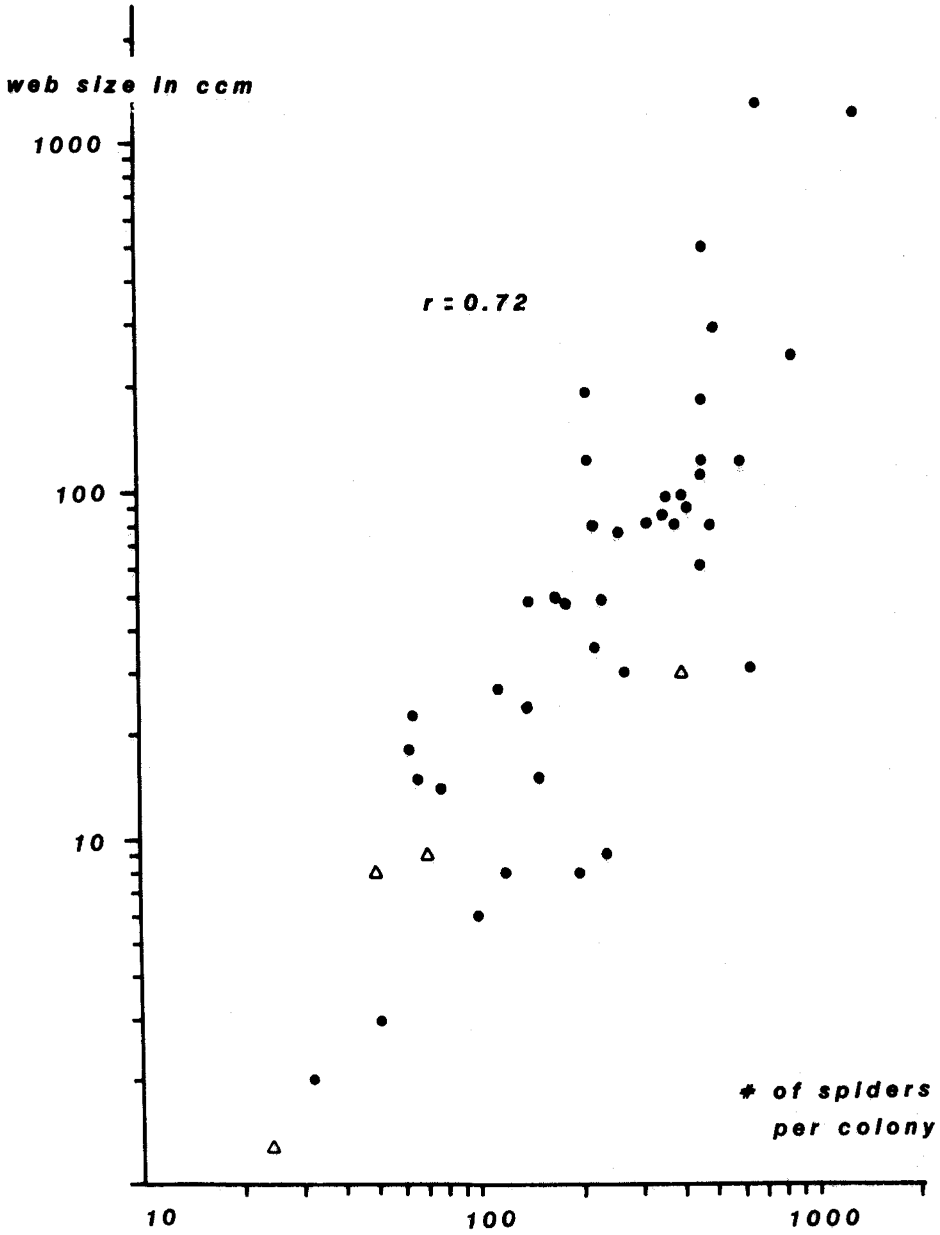

Fig. 2.—Scattergram and correlation coefficient (r) of the size (volume) of the retainer web and the number of *Anelosimus eximius* inhabiting it. Volume was calculated using the equation 2:3 phi*a*b*c (a = height of bowl, b = width, c = length of bowl). The formula of the regression line was y = x*a+b. Each point represents one colony of *A. eximius*, the triangles represent colonies of the subsocial congeneric *A. juncundus*.

temperature nor humidity changes drastically inside the forest (ESPI report 1976), the presence or absence of rain and wind, as well as the seasonal distribution of prey insects (Robinson and Robinson 1970, Wolda 1977, 1978) allow the assignation of different environmental qualities to each season (Vollrath 1980); in the lowlands, for instance, March is a rather severe month for spiders (Lubin 1978). The effects of the seasons are less pronounced in the higher elevations, especially in the cloud forest, where light afternoon showers fall throughout the year (unpubl. RENARE data).

Suitable colonies were collected in the field and taken into the laboratory where they were analyzed: the spiders were extracted, classified, and counted. Classification was by size, and the different size classes were presumed to represent instars (see Fig. 1). Suitability was judged by the apparent health of the colony and by the ease with which the web could be tipped into a large plastic bag without the loss of animals. Sometimes the area underneath a web was covered with sheets which were later inspected for escapees, showing that only strong shaking initiated escape responses in all but the first and second instar spiderlings. Older instars escaped in similar proportions, which permits the comparison of all collection data (even in the few cases where spiders might have escaped during collection), as long as the data are represented as percentages. In addition to sampling whole colonies (data in Table 1) I censused other colonies in the field, without disturbance, repeatedly over a one year period, counting spiders in situ. Most of these data were not used in the analysis (but see Fig. 7), since rarely was the vision good enough to count and classify all spiders.

The calculations of biomass (wet weight) use weight measurements of 5 live spiders of each size class, which gave the following mean weights: size class 1 = 0.5 mg, 2 = 1 mg, 3 = 2 mg, 4 = 3 mg, 5 = 7 mg, female (6) = 15 mg and male = 7 mg (Vollrath unpubl.). I give no standard variation since the spiders had been preselected to be of roughly medium weight for their size class, as judged by the state of their abdomens.

RESULTS

Effects of seasonality.—The three sites: lowland, intermediate and high elevation were compared in the effects they exert on the population dynamics of *A. eximius*. The colony cluster on the El Llano-Carti Road initially (April 1978) consisted of over 20 large (about 2000 spiders each) to medium sized colonies (about 600 spiders each). Later (June) many new colonies were founded in the vicinity by single females which were often joined by other females. During the time from May until September gravid females emigrated from most of the old (mature) colonies (Vollrath 1982), departing from the top of the vertical threads. It is unusual for *Anelosimus* to be active during the day in these parts of the nest, and since I only twice saw a male here, I assume that males do not take part in the emigration. In September the colonies in this site began to dwindle, with many sickly or dead spiders hanging in the webbing. It is conceivable that a virus had spread and contaminated all or most colonies. At the end of December only two nests were left, much reduced in size. Because of the combined effects of emigration and possible epidemic, the interpretation of data from the El Llano site will only be referred to qualitatively.

Seasonal changes in the composition of size classes were more apparent in the lowland sites of Bohio and Pipeline than in the highland El Valle sites (Fig. 3 and Table 1). The lowland colonies contained very few egg sacs in April, the end and severest month of the dry season. With two exceptions however, they had plenty of egg sacs throughout the rainy season and at the beginning of the dry season. In March/April I found only a single egg sac in 4 colonies, the mean

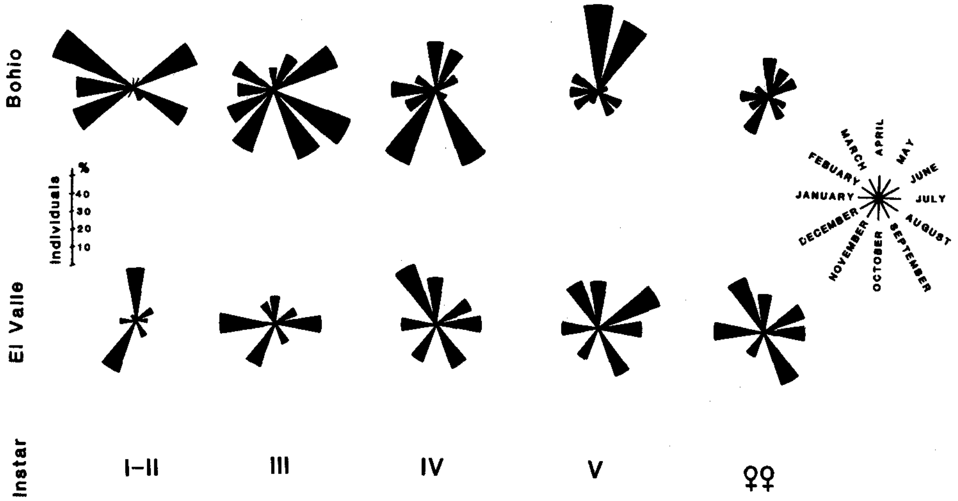

Fig. 3.—Size class composition of colonies collected in the lowland (Bohio) and the highland sites (El Valle). Each circular histogram represents the annual cycle (reading clockwise), the length of each sector gives the relative proportion of spiders (in percent) of the particular size class (indicated by the roman numeral) at the sampling month (compare Table 1).

number of egg sacs in 4 colonies was 6 in August/September (Table 1a). The El Valle colonies, in contrast, had egg sacs throughout the year: in 5 high elevation colonies I found a mean number of 6.4 egg sacs during March/April, and a mean of 15.2 during August/September (Table 1c). Even the El Llano site had a fair number of egg sacs in April (Table 1b).

The proportion of young in each colony also gives some indication about the seasonality of reproduction. In the lowland sites no first or second instar young were found in April/May and very few in September/October. In the highland sites young were present throughout the year. In both sites the composition of other instars varied. This is not astonishing since colonies even at the same site seemed to differ from one another, in exposure to the elements, to prey, parasites and predation. However, in the lowland site fourth and fifth instars showed marked preponderances during certain times of the year, fourth instars at the end of the rainy season and fifth instars at the beginning of the rainy season. In both sites adult females were present throughout the year, so were males. The difference between the sites is most easily expressed by the coefficient of variation (CV, Simpson et al. 1960) of the instar composition. The CV for the lowland colonies was CV = 60 (n = 14), for the high elevation colonies it was CV = 36 (n = 14): the colonies in the elevation site showed greater uniformity throughout the year than those in the lowlands.

The proportional representation of instar numbers masks the true extent of the difference between the two sites. The seasonal investment in reproduction is better represented by the proportion of a colony's biomass tied up in the different age classes, which depicts the differences better (Fig. 4). The seasonal aspect in the lowland colonies is apparent in the biomass distribution of the early instars which is concentrated in February and September. In the lowlands, most of a colony's biomass at the beginning of the dry season consists of females, while during the dry season a large proportion consists of young. At the beginning of the next rainy season nearly all biomass is tied up again in subadult or adult females,

Table 1.—Colony composition at the three study areas. The sample month is given first, followed by the total number of spiders (spids), the number of adults (ads), the number of males (♂♂), the adult sex ratio (ratio = males as proportion of adults), the number of egg sacs (egs), and finally the ratios of females to egg sacs (♀: eggs) and males to egg sacs (♂: egs). Lowland colonies were collected in: Bohio (a), Pipeline Road (b), Anchiote Road (c), Bayano-Mahe (d); two colonies are shown, which were not collected, but where censused accurately in the field (*).

BIOHIO (a), PIPELINE (b), ACHIOTE (c), BAYANO (d)

Month	spids	ads	♂♂	ratio	egs	♀:egs	♂:egs
Jan. (b)	493	74	12	0.17	21	3.0	0.6
Feb. (a)	413	32	4	0.13	0	—	—
March (d)	379	51	10	0.2	0	—	—
April (c)	213	90	6	0.07	0	—	—
(a)	574	72	12	0.13	1	60.0	12.0
(a)	365	86	14	0.17	2	36.0	7.0
May (b)	787	147	30	0.2	8	14.6	3.8
June (a)	425	65	3	0.05	11	5.6	0.3
(d)	459	160	24	0.15	17	8.0	1.4
Aug. (a)	844	95	4	0.04	1	91.0	4.0
(a)	999	120	5	0.04	9	12.9	0.6
Sept (b)	476	8	7	0.5	0	—	—
Nov. (a)	228	46	3	0.07	14	3.1	0.2
Dec. (b)	398	55	13	0.25	5	8.4	2.6
x̄	503	79	10.5	0.16	6.4	24.3	3.3
± sd	227	42	8.1	0.12	7.1	29.5	3.8

EL VALLE

Month	spids	ads	♂♂	ratio	egs	♀:egs	♂:egs
Jan.	423	117	10	0.08	19	5.6	0.5
March	463	147	11	0.07	6	22.7	1.8
	598	172	19	0.11	11	13.9	1.7
April	671	146	14	0.1	10	13.2	1.4
	268	56	12	0.2	9	4.9	1.3
	631	123	24	0.14	13	8.4	1.9
June	365	59	12	0.2	2	13.5	6.0
	485	111	11	0.1	3	33.3	3.7
	1002	340	32	0.09	76	4.1	0.4
July	738	168	17	0.1	40	3.8	0.4
	298	77	12	0.17	3	21.7	4.0
Sept.	145	22	4	0.17	8	2.3	0.5
	386	50	12	0.25	21	1.8	0.6
Nov.	619	64	16	0.25	4	12.0	4.0
x̄	506	118	14.7	0.15	16.1	12.2	2.1
± sd	221	80	6.8	0.06	20.0	9.7	1.7

EL LLANO-CARTI

Month	spids	ads	♂♂	ratio	egs	♀:egs	♂:egs
March	1305	301	42	0.14	0	—	—
April	434	43	15	0.35	14	2.0	1.0
	1226	128	10	0.06	7	12.8	0.7
May	190	61	9	0.08	5	6.8	0.6
July	490	90	14	0.18	16	6.4	1.1
	475	232	5	0.18	41	46.4	8.2
Aug.	210	26	3	0.12	2	7.7	0.7
Sept.	379	189	21	0.11	14	13.5	1.5
Sept.*	(200	52	0	—	0	—	—)
Nov.*	(270	18	12	0.66	0	—	—)
x̄	588	134	14.9	0.15	12.4	13.7	2.0
± sd	433	98	12.4	0.09	12.9	15.0	2.8

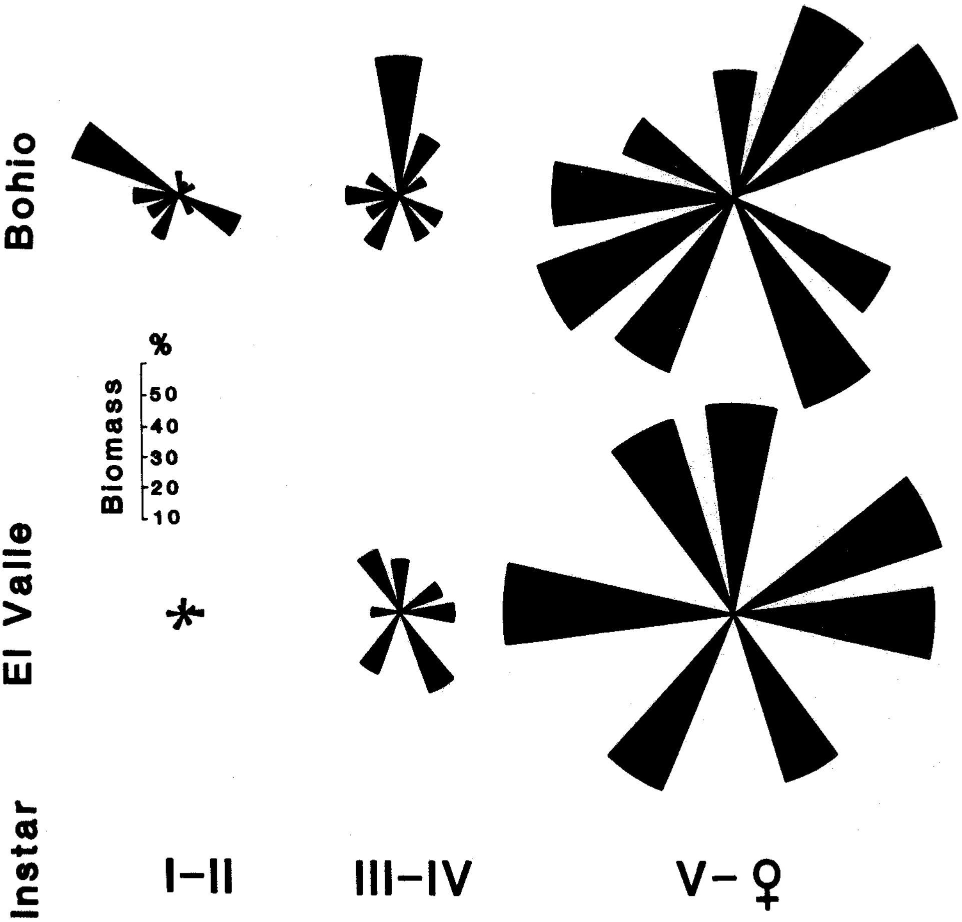

Fig. 4.—Representation of the distribution of colony biomass in the different size classes. The biomass was calculated using the mean wet weight of 5 spiders for each class (see methods). For explanation of the circular histograms see Fig. 3.

ready to reproduce and rear a second generation. No such variation was found in the biomass distribution of colonies in the highland sites.

The quantitative observations on 38 colonies are supported by qualitative observations on about a hundred colonies which were not disturbed (Vollrath unpubl.). They allow the generalization that in different parts of the country colonies in similar habitats show similar trends in egg production and instar representation, with pronounced seasonal influences in the lowlands.

Colonies in the El Llano site were intermediate in their reproductive cycle (Table 1b). The average colony size was similar in all three sites. The average ratios of adults to juveniles was also quite similar between the two upland locations: 0.23 in El Llano and 0.23 in El Valle. It was considerably lower in the lowlands (0.16) where colonies generally had a smaller proportion of adults. The average number of egg sacs produced in the upland site was intermediate (12) between the altitude site (16) and the lowlands (6). The ratio of adult females to egg sacs was also intermediate (14) when compared with the lowlands (24) and the highlands (12). These differences are not statistically significant because of the large variation in all sites.

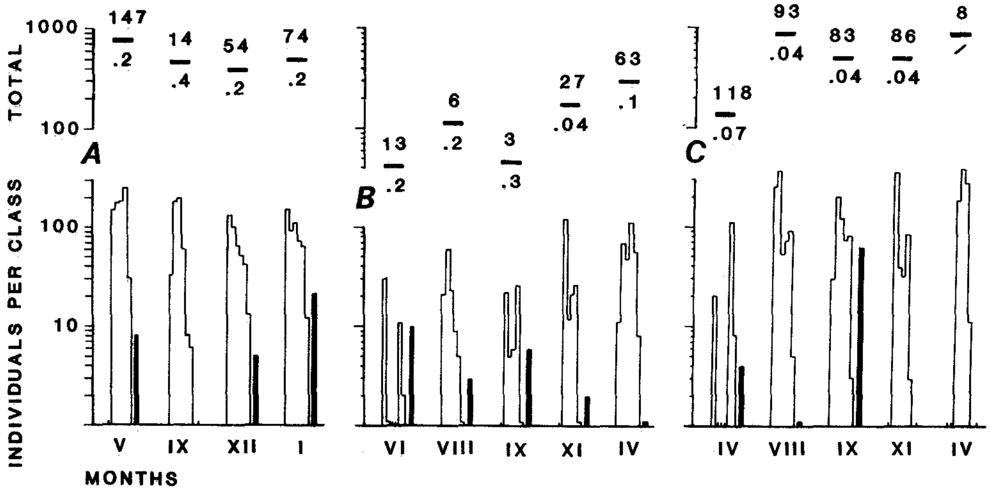

Fig. 5.—Dynamics of three *Anelosimus eximius'* colonies censused repeatedly in the field at the lowland sites of Bohio and Pipeline Road in 1978-1979. The X-axis denotes the month (roman numerals). The upper horizontal bars show the total number of spiders in the colony. The number above each bar give the number of adult spiders, numbers under the bars denote the sex ratio (male proportion of adults). The dark columns give the number of egg sacs. The actual numbers of spiders of the different size classes (1 to 5 and (♀♀) is shown for the sample months by histogram outlines.

In order to study the dynamics of individual nests, many webs were examined regularly in the field, with minimal disturbances. Only in few cases was the visibility inside the colony consistently good enough to view 80 to 90% of all spiders, thus allowing me to use these data. Figure 5 shows the changes in the population of three colonies in a lowland site during the course of one year. Colony A contained no egg sacs in September, colonies B and C had few egg sacs in November and April. The age profiles of the three colonies differed in several aspects, which may be explained by the differences in size. Colony A, initially being the largest with 1000 individuals, maintained a stable age distribution throughout the year. Both colonies B and C were growing in size, B was the smaller of the two. The instar composition of the two colonies B and C was similar in most months, often showing a depression in the middle instars. No similar depression was found in the age structure of the mature colony A. Other colonies, monitored with less accuracy (Vollrath unpubl.), showed similar variations in egg production and age structure, again possibly correlated with colony size.

In the El Valle site *Anelosimus juncundus* also seems to reproduce throughout most of the year. There I found many nests, each containing one adult female with eggs in the months of April, June, July, September and November. In the other sites *A. juncundus* may be seasonal, but I found too few individuals to make a definite statement. In the El Llano site 6 females and egg sacs were found in July, and in the lowland site of Cerro Galera I found only two females with eggs, in May. Although *A. juncundus* was at times found abundantly in the high elevation and the intermediate sites, it appeared to be rare in the lowlands.

Sex ratios.—In all three habitats the adult sex ratios were highly variable but (with a few notable exceptions) heavily biased in favor of females (Table 1, 2). There were no differences in the mean sex ratios between the three habitats (0.16,

Table 2.—Composition of new foundations in the El Llano-Carti site. The July column shows the number of first instar spiderlings. 64 days later, in September, all had progressed to the fourth instar, when the males show their sex. Only 4 males were then still immatures (included in ♂♂), the other males had just matured. Immature females are denoted by IV (fourth instar).

	July	September			mortality	sex ratio
		IV	♀♀	♂♂		
	32	12	8	4	25%	0.17
	21	0	9	2	48%	0.18
	78	4	30	2	54%	0.06
	39	12	8	4	38%	0.17
	40	20	4	2	35%	0.08
	31	6	6	1	58%	0.08
	41	5	15	2	46%	0.09
$\bar{x}$	40	8	12	2	43%	0.12
± sd	17	6	9	1	11%	0.04

0.15, 0.15). On average, colonies in all three sites contained about five females for every male.

We have seen that pronounced local environmental factors influence the reproduction and instar composition of colonies. It is conceivable that the large variance in the sex ratios could be the result of environmental influences, comparable to the effect of temperature on the sex determination of a turtle egg (Bull 1981). Such effects might show in a correlation between the colony sex ratio and the time of year. No significant correlation was found (Fig. 6a), suggesting that a direct seasonal influence on the sex ratio is not likely. What about indirect influence?

Seasonality expresses itself in changes of the abiotic as well as the biotic factors. In the lowland the exposure to desiccation by wind and sun increases during the dry season when the trees are shedding their leaves. At the same time the number of prey decreases while predation presumably increases (Robinson and Robinson 1970). Inside a nest of *A. eximius* these factors are probably buffered, the degree of insulation depending on colony size. For example, on a sunny afternoon in the dry season the relative humidity was 74% inside a (1000 individual) lowland colony, when outside it was 60% (dry/wet bulb temperature measurements). Large colonies have large collections of leaves which provide more shelter and also chambers of relatively constant conditions. Large colonies may also be affected less by predation (Fig. 5, and Vollrath and Windsor in press).

A scattergram of colony size plotted against the sex ratio shows no significant trend if all data are lumped (Fig. 6b). However, a weak correlation ($r = 0.36$) was found for the high elevation site, where the sex ratio of larger colonies was more female biased. This correlation improved and became significant ($r = 0.663$, $0.05<P<0.01$) when the number of mature spiders only (instead of all individuals of a colony) was plotted against the sex ratio (Fig. 7a). If analyzed this way, colonies in the lowlands which were censused repeatedly also showed some correlation ($r = 0.479$, $0.1<P<0.05$, Fig. 7c), whereas still no correlation was found for the collected lowland colonies (Fig. 7b).

Colony size can be taken, to a very limited degree, as an indicator for the age of a colony. Isolated small nests are generally new foundations, isolated large nests are several generations older (Vollrath 1982). Since most of the colonies

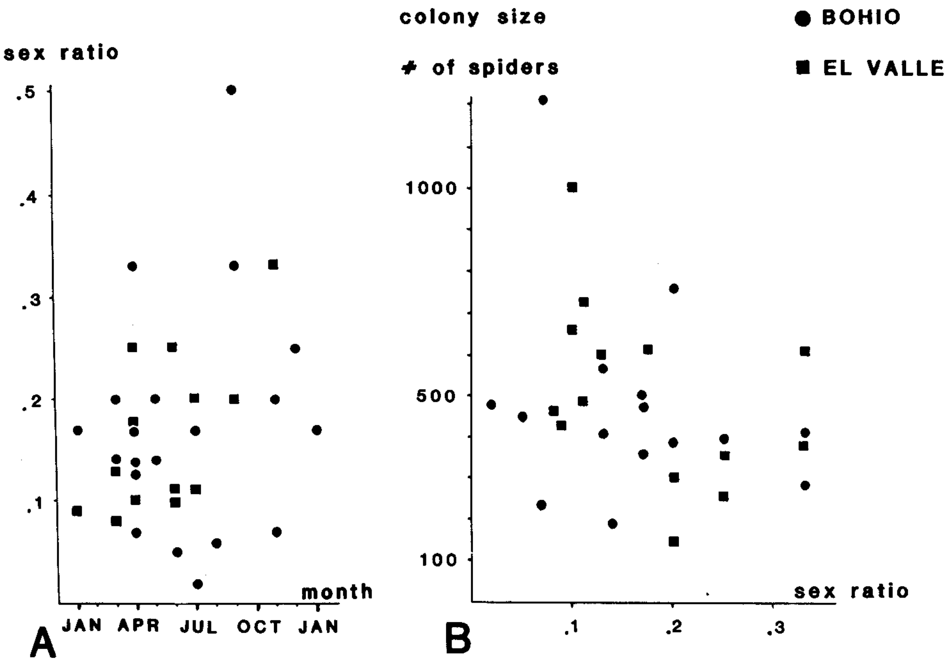

Fig. 6.—Scattergrams of: (A) colony sex ratio and the time of year, and (B) colony sex ratio and colony size. Sex ratios were calculated as the male proportion of all adults.

sampled had been taken from colony clusters, they may have been recent offshoots of much older foundations. None of the new foundations that I either observed to occur naturally or which I experimentally started, survived for longer than 6 months (Vollrath 1982). However, I do have, from some of these natural foundations, some information on the sex ratios of new colonies (Table 2). The mean ratio (± s.d.) in these colonies was 0.12 (± 0.04), this is lower than the primary sex ratio of 0.08 (± 0.01, Vollrath 1986) but higher than the average ratio of mature colonies (0.15 ± 0.09).

Reproduction is measured by the number of offspring produced, and we saw that reproduction was clearly seasonal in the lowland sites and may have had a seasonal component in the highland site. Reproduction is presumably also a joint effort of the male as well as female since no spider is known to be parthenogenetic. Although the sex ratios showed seasonal trends, the possibility remains that a correlation may be found between reproductive effort and the relative abundance of either sex. The ratios of males or females to the number of egg sacs present in a colony are given in Table 1. There were no differences in the sex ratios between the two sites. There were, however, pronounced differences in the average number of egg sacs produced by colonies in the two sites, production was more than double in the altitude sites when compared with the lowland sites (16 versus 6). Accordingly the ratio of females to egg sacs was also lower: in the altitude site one egg sac was produced for every 12 females, in the lowlands it was one egg sac for every 24 females. A similar trend was found in the ratio of males to egg sacs. This analysis of colony composition and presence of egg sacs shows that the ratio of females to egg sacs was generally more than 10 to one, whereas the ratio of males to egg sacs was roughly two to one (Vollrath 1986).

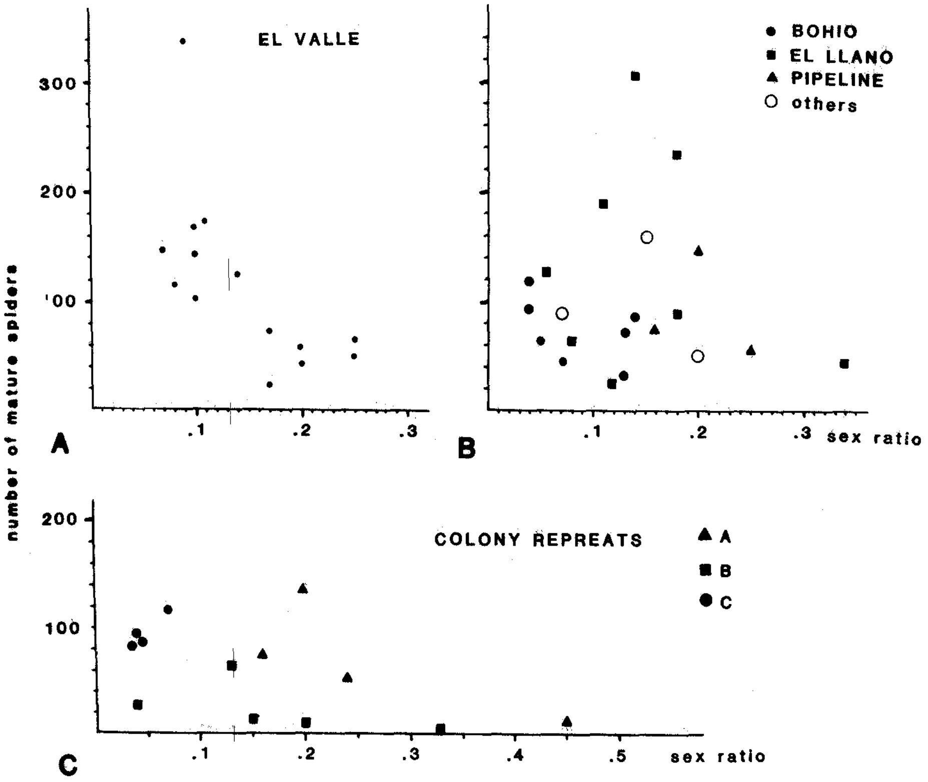

Fig. 7.—Scattergram of adult colony size and sex ratio for (A) highland colonies, (B) lowland and altitude colonies, and (C) colonies in the lowlands which were censused repeatedly. A and B represent data from Table 1, C represents the colonies from Fig. 5.

DISCUSSION

Population dynamics and seasonality.—It emerges from the data on instar composition of colonies, and even more from the calculations of colony biomass, that the populations of *A. eximius* had different dynamics in the two main sites, highlands and lowlands. It is most likely that these differences were due to the differences in environmental parameters, which had a clear seasonal component. It cannot be inferred from the data that the differences in colony composition were due entirely to abiotic factors. Heavy rainfall, for example, destroys the capture threads and may force "the colony" to spend much energy in frequent rebuilding during the rainy season. On the other hand, active spiders dessicate quickly in very dry conditions (Davies and Edney 1952). In order to conserve water in the dry season colony activities are possibly reduced to the extent of neglecting the web, thus foregoing prey capture and nutrient uptake. However, it is more likely that a combination of biotic and abiotic factors was responsible for the observed differences in the two sites. Most prey insects, for example, have activity cycles clearly delineated by the seasons (Wolda 1977, 1978, ESPI report 1976). Predators, especially predatory arachnids and insects, will presumably also show seasonality to match the temporal distribution of their spider prey. Lubin (1978) has shown that most solitary spiders in the lowland forest of Panama have distinct seasonal distribution and reproduction. My study suggests that the social spider *A. eximius* is less seasonal than its solitary sympatrics, which practically disappear from the habitat in the late dry season.

The seasonality of *A. eximius* expresses itself most strongly in the presence of egg sacs, it appears that in the lowlands reproduction stops during the height of the dry season, in March and April. The highland colonies, on the other hand, had egg sacs all year round. Although egg production was markedly different between the two sites, the sex ratios showed no comparable trends.

Sex ratios and environment.—The sex ratios in colonies of *A. eximius* were heavily biased in favor of females (Overal and Ferreira 1982, Christenson 1984, Aviles in press, Vollrath 1982, Vollrath 1986). In some reptiles the sex ratio in a population can be affected by the environment during the time of egg development (Bull 1981), because ambient temperature has a modifying effect on the hormonal control of sex determination. In spiders the sex is not determined hormonally but by the chromosomal set of each cell individually [(viz the presence of gynandromorphs, comparable to insects (White 1973)]. Still, abiotic factors in the environment could conceivably influence the sex determination of a developing egg. This possibility seems unlikely since the observed variation in sex ratios, although quite large, showed neither seasonal nor locality differences (Table 1). Moreover, colonies collected at the same time in the same location showed as large a variation as colonies collected at different times in different locations.

If abiotic factors are ruled out, could possibly biotic factors be responsible for the sex ratio bias? Three main agents of biotic influence can be distinguished: parasitism, predation and prey (nutrition). Of these nutrition is the most difficult to separate from abiotic effects, since the activity of prey insects is in itself often triggered by abiotic factors. Direct, long-term observations of prey capture for the discussed colonies is lacking (but compare Nentwig 1985), therefore prey intake was deduced from colony size, for this spider biomass may be a better measure than number of individuals. Since environmental conditions might have been unique at the time when the measured sex ratio of a colony was fixed (i.e. when the adult spiders developed), adult numbers or biomass would have to be compared with the sex ratio of each colony. However, different rates of the mortality of males and females could easily mask any effect nutrition might have had.

The highland sites showed a clear and significant negative correlation between the number of adults and the sex ratio. A similar effect was apparent in the three colonies censused repeatedly in the lowland site, but it was not visible in the other lowland colonies. How can we explain the observation that colonies with fewer adults contained relatively more males? If we assume the same mortality for both sexes, this observation would lead us to deduce that fewer male eggs were laid at times when prey was abundant, and the colony was growing. Such an effect would be independent of absolute colony size, as a comparison of the altitude and the censused colonies shows. However, could not all the data, including the observations on all lowland colonies, be better interpreted by the alternative assumption that males and females experience different mortality?

In *A. eximius* the average primary sex ratio was much lower than the average adult sex ratio observed in the field (Vollrath 1986), this suggests that many females have either died or left the colony between hatching, maturation, and older age. *A. eximius'* males rarely venture far from the retreats, and they do not assist in web construction nor in prey capture. The females, on the other hand, expose themselves to predators during the daily routine of capture-thread construction, and to injury during the attack and subduction of potentially dangerous prey insects (Vollrath and Rohde-Arndt 1983). They may even defend the colony with considerable risks to their own lives (Vollrath and Windsor in press). It would appear that female mortality was on average twice male mortality (difference between primary and actual sex ratios: 0.08 vs 0.15), if the hypothesis of higher female mortality is correct. Such an interpretation of the sex ratio data would be supported by the observation that large colonies survive better than small colonies (Vollrath 1982), an indication that in nests with many "workers" more of them survive. This is supported by the observation that small foundations had on the whole a lower mean sex ratio than the larger mature colonies (0.12 vs 0.15). The data on new foundations comes from nests in which the sexes are about to mature, or have just done so (Table 2). It appears that at this moment already more female than male spiderlings have died. After maturation this ratio shifts even more towards the males (to 0.15), since male and female adults are presumably more dissimilar than the juveniles.

Instead of mortality, female emigration might account for the rate of female "disappearance", which was 50% higher than that of the males. In *A. eximius* emigration seems to be a well defined phenomenon, associated with a particular behavior pattern (Vollrath 1982). Females move into the upper strands of the capture area, where they depart, using their floating dragline as a bridge. This behavior, combined with the observation that it occurs during the morning, a time when the spiders normally are at rest in the retreats, makes emigration quite obvious. The many hundreds of females I observed moving in the capture threads prior to departure were only twice joined by a male, which both times retreated back into the colony. Only one of the 380 single or multiple female foundations examined contained a male which presumably had followed the females to their new nest a few meters away from the likely parental colony (Vollrath unpubl.). Emigration seems to occur at specific times of the year and the day, and it is unlikely that females leave in any significant numbers at other times (Vollrath 1982). Males presumably leave their parental colony only rarely, and possibly accidentally. It is concluded that emigration is not a likely explanation for the observed bias in the sex ratios.

Summarizing the discussion on the sex ratio bias I want to conclude that the sex ratio in *Anelosimus eximius* is probably not influenced by abiotic environmental factors. The strong bias in favor of females is due to the fact that many more female eggs are laid. This effect of a biased primary sex ratio is slightly softened by higher female mortality due to predation, which is a biotic vector of the environment with considerable local and temporal variation.

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