

Biology of a Paraguayan colonial orb-weaver, *Eriophora bistriata* (Rengger) (Araneae, Araneidae)

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Summary

Colonies of the Paraguayan *Eriophora bistriata* were found to be highly social. Rhythmic activity cycles were found to be present with prey capture occurring nocturnally. Individual orbs were spun daily, with site fidelity decreasing over time. Spiders exhibited co-operative behaviour in the construction of the web superstructure, and in the capture of large prey. *E. bistriata* was found to be univoltine, with siblings developing synchronously. After the last moult, females dispersed to lay eggs. The population dynamics, and the advantages of group living to this species are discussed.

Introduction

For decades, Paraguayan artisans have woven natural fibres into an intricate fabric known as 'ñandutí', which in the native Guaraní language literally means spider web. To view the ñandutí, one could easily imagine a colony of orb-weaving spiders. Colonial orb-weavers do, in fact, inhabit Paraguay, and probably served as the primary model for these weavings. Early in the 19th Century, studies were also conducted on the possibilities of exploiting the silk spun by these colonies in commercial textile production (Holmberg, 1874a).

Rengger (1835, 1836) was the first to describe a colonial araneid from Paraguay, naming it *Epeira bistriata*. Mello-Leitão (1932) designated it *Eriophora*

bistriata in his generic revision. However, Rengger (1835, 1836) also proposed the name of *Epeira socialis* for the same species, and it is this junior homonym which is the better known, due to its use by Simon (1891). Holmberg (1874b) also designated a colonial araneid as *E. socialis*, but it is uncertain if this species is the same as Rengger's. In order to avoid ambiguity, Mello-Leitão (1932) proposed the name *Araneus sermoniferus* to supplant Holmberg's designation. Specimens of *E. bistriata* from this study have been deposited in the Museum of Comparative Zoology of Harvard University.

Early naturalists (Azara, 1809; Rengger, 1835, 1836; Masterman, 1869, 1891; Darwin, 1845; Goldi, 1892; Holmberg, 1874a, 1874b) reported on the gregarious behaviour of a large, black colonial araneid in southern South America. These early reports were often discredited by prominent arachnologists, notably McCook (1890), Walckenaer (editing Azara, 1809), and O. P.-Cambridge (1870), and were not generally accepted by the scientific community until Simon (1891) provided his support.

This paper re-examines some of the early observations on the behaviour and biology of *E. bistriata*, and attempts to quantify some of the more pertinent aspects of the ecology, biology and behaviour of this species, in particular, those aspects related to its sociobiology. Studies were conducted in San Lorenzo, Paraguay, from December 1975 until August 1976 (Lat. 25° 21' 23" S., Long. 57° 33' 36" W), with supplementary laboratory observations carried out at Rutgers University. In the field, *E. bistriata* was found to occur in urban and semi-urban habitats as far east as Caacupe (Lat. 25° 24' 00" S., Long. 59° 08' 00" W.), but it probably occurs well into southern Brazil (Mello-Leitão, 1932). Southern ranges extend at least to Santa Fé, Argentina (Darwin, 1845), while to the west *E. bistriata* is found at least as far as Tucumán, Argentina (R. B. Roberts; pers. comm.). *E. bistriata* is especially abundant in the Gran Chaco Basin, and probably ranges north to a limit south of Bolivia. In the mesic habitats east of the Paraguay River, *E. bistriata* was found in open woodland and orchards, while west of the Paraguay River it was found in palm (*Copernicia* spp.) in the lower pantanal, and in isolated trees in the more xeric upper Chaco (N. Guerrero, pers. comm.). Judging from the number of

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specimens in museums, *E. bistriata* is probably very common (H. W. Levi, pers. comm.).

Methods

The spatial distribution of individuals in one colony was studied by counting the number of spiders present in one 2.5 m high x 2.5 m wide section of the communal capture web close to the daytime retreat. Data were compiled for each spider in this web section for: (1) its height above the ground; (2) the diameter of the individual orb web, if present; (3) the distance to the nearest orb; and (4) the distance to the nearest spider. Illumination for these nocturnal counts was provided by a hand torch which produced no observable behavioural modifications. Additionally, the vertical distribution of individual orbs was examined by counting the number present in each 0.5 m increment of height.

The presence or absence of a hierarchical pattern of web construction and location was studied by individually marking 13 spiders with a drop of tempera paint on the dorsum of the opisthosoma. No adverse effect of marking was observed on either the behaviour of the individuals marked, or on the behaviour of unmarked conspecifics toward them. Changes in the spatial locations of the marked spiders were followed until the first began to moult.

Prey capture was examined over 150 observation periods, which ranged from 0.5 to 2.0 hours each. Prey captured in the individual orbs were measured to the nearest mm of body length, and then converted to a ratio of spider size (prey length/spider length). This ratio was used to study the effect of prey size on co-operative prey capture and communal feeding incidents in incipient and mature colonies, as preliminary observations had indicated that both were related to prey size.

Colony densities, population and dispersal were studied in a 480,000 m² plot (6 x 8 city blocks). Colonies were found, their location marked on a grid map, and then visited regularly to census colony populations. Counts were conducted at night with the aid of a hand torch. The dispersal of the colony founding females was also followed with the same series of grid maps. The rate of dispersal was calculated by the formula of Clark (1962):

$$\text{rate of dispersal} = \frac{(d^2)}{N}$$

where d = distance of spider from nest, and N = total number of spiders observed. The heterogeneity of dispersal of the colony-founding females was estimated by the formula of Dobzhansky & Wright (1943):

$$\text{heterogeneity of dispersal} = \frac{N \sum_{p=0 \rightarrow 1} d(p^4)^{n_p}}{\left(N \sum_{p=0 \rightarrow 1} d(p^2)^{n_p} \right)^2}$$

where n_p = total number of spiders found at the same distance from the daytime retreats, d_p = distance of spider from the daytime retreat (p), and N = the total number of spiders found. Additionally, the number of females giving rise to viable colonies was recorded, and from these data, as well as data on individual clutch sizes, the net reproductive rate (R_0) was estimated.

Two incipient colonies were established in cages 1.0 m high x 0.5 m wide x 0.5 m long under laboratory conditions in August 1976. Observations were made on the degree of cannibalism and developmental synchrony of the cohorts, as well as basic data on the life cycle. Discarded exuviae were recovered and measured with an ocular micrometer to assess individual growth patterns.

Results

Physical structure of colonies

The physical structure of colonies of *E. bistriata* was found to be comprised of two basic parts: the daytime retreat, and the nocturnal capture web. The daytime retreat was usually located on a tree branch, 2 to 5 m above ground level, and consisted of a variable amount of silk which housed the spiders during their communal roosting. In the majority of colonies observed, little silk encompassed the communal roost, with the clumped spiders taking on the appearance of a huge, black mass. Some colonies in the more xeric areas of the Chaco Basin had a greater amount of ensheathing silk, although these, likewise, were not completely

enclosed. Roosts were encountered in semi-open wood or shrub land, but were never found in closed canopy forests. One roost was found below the bulb of a street lamp.

From the daytime retreats, one to many communally spun thick silk threads radiated out to other nearby trees or shrubs of the immediate habitat. These threads often ran 30 m or more from the daytime retreat. From these threads, a network of individual orb webs were spun at night to form the nocturnal capture web.

Activity cycles

At dusk, a few spiders were found to leave the daytime retreat and run back and forth along the thick threads, strengthening them by spinning more silk. As this activity progressed, the mass of clumped spiders in the daytime retreat slowly began to break up. Other spiders then began to leave the central retreat along the thick threads. These outgoing spiders spun silk to nearby trees and shrubs, or to the lower herbaceous ground vegetation, thus forming a network of secondary supporting threads. Within this superstructure, individuals began to spin individual horizontal orb webs. Individual orbs were structurally much like those of *Araneus*. The uninterrupted radii were spun first, then the viscous spirals, beginning from the outer margin. Within 60 min., the last of the individual orbs were completed. Individual orbs were spun with a distinct preference exhibited for the higher parts of the silk superstructure (Table 1). The completed network of webs covered 100 m² or more of surface area. However, due to the placement of the individual orbs,

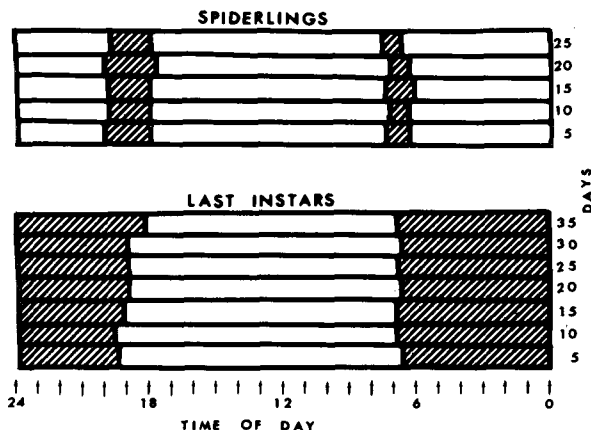


Fig. 1: Activity cycles of *E. bistrriata* for incipient and adult field colonies. Hatched = active phase (orb web construction and prey capture); blank = clumped in daytime retreat. Days refer to days of observation.

gaps existed through which flying insects passed without becoming entrapped.

With the approach of dawn, the spiders migrated into the daytime retreat. The secondary supporting threads and the individual orbs were gathered in by the spiders during their return to the daytime retreat, leaving only the principal connective threads. Individual orbs were dismantled and eaten sector by sector, much like the actions described by Breed *et al.* (1964) for *Araneus diadematus*. Upon entering the retreat, the spiders began to clump one upon another by grasping the prosoma and opisthosoma of another and depressing its body. As the last of the spiders entered the retreat, a compact clump of individuals was formed.

Activity cycles were markedly rhythmic, with the same rhythm and behaviours observed in the first and last instars (Fig. 1). Early instars often went out, spun orbs, and then reclumped, with prey being left for re-collection in the morning. Although this varied somewhat from the activity cycles of the later instars (Fig. 1), both initiation and termination of prey capture activity in juvenile and adult colonies showed the same rhythm.

Feeding behaviour and prey

As the spiders constructed individual orb webs, most of the prey was ensnared through the actions of individual spiders. When prey size was small

Height (m)	No. of orbs	Frequency of occurrence
< 0.5	18	0.0110
0.5 - 1.0	16	0.0098
1.0 - 1.5	112	0.0682
1.5 - 2.0	704	0.4290
2.0 - 2.5	672	0.4095
> 2.5	119	0.0725
Total	1641	1.0000

Table 1: The vertical distribution of individual orbs in one field colony of *E. bistrriata* over a two month period.

relative to spider size, it was usually wrapped in silk and left to be consumed when the silk was gathered in and eaten at dawn. The prey was consumed with the silk, and was not carried to the daytime retreat. Wrapping was accomplished by utilizing the nearest available sticky silk, which the spider took with the hind legs and wrapped the prey several times. Prey was often immobilized by bites prior to ensheathment. Smaller prey were usually left to entangle themselves, and were likewise consumed when the silk was gathered in at dawn.

Large prey, relative to the size of the spider, were usually immobilized immediately with quick bites. If the prey was very large, adjacent spiders joined in to subdue its movements. Prey was then consumed at the site of capture, often with many spiders joining the captors to feed communally (Table 2). The number of spiders feeding on any one prey item was related to prey size. In no instance was prey observed being transported to the daytime retreat.

Prey size and abundance apparently corresponded with the instar development of the spiders, both of which were probably a function of seasonality. During summer and early fall, prey was abundant, especially Diptera, Homoptera, Hemiptera, Lepidoptera, Orthoptera and Hymenoptera. However, there were intermittent abundances of alate reproductives of termites and ants. The dispersal of the females and subsequent death of the adults in the fall corresponded with harsher weather conditions, and a

Prey size index	Frequency of numbers of spiders feeding						N
	1	2	3	4	5	> 5	
0.10	1.00	0	0	0	0	0	344
0.25	1.00	0	0	0	0	0	257
0.50	1.00	0	0	0	0	0	284
0.75	0.89	0.11	0	0	0	0	185
1.00	0.93	0.07	0	0	0	0	229
1.25	0.76	0.20	0.04	0	0	0	91
1.50	0.51	0.32	0.12	0.05	0	0	100
1.75	0	0.27	0.44	0.19	0.07	0.03	74
2.00	0	0	0.16	0.23	0.36	0.25	41
2.25	0	0	0	0.36	0.23	0.41	23
2.50	0	0	0	0.12	0.44	0.44	9

Table 2: Relative frequencies of solitary and communal feeding in relation to prey size in colonies of *E. bistrata*. Prey size index = prey length/spider length.

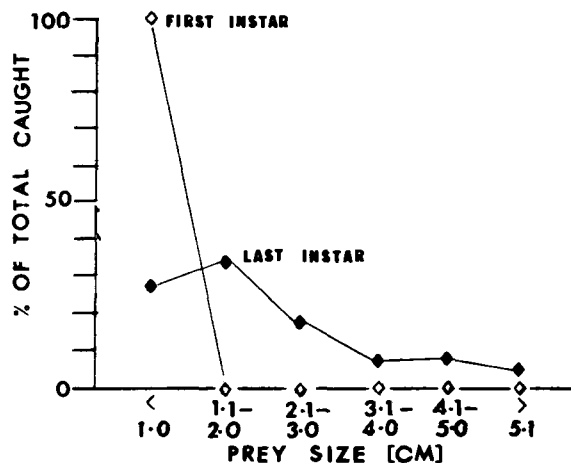


Fig. 2: Frequency of prey sizes in orbs of adult and incipient colonies of *E. bistrata* in central Paraguay.

subsequent decline in prey abundance. The eclosion of the spiderlings in the spring coincided with the abundance of many small insect prey, notably nematoceros and cyclorrhaphous flies, and reproductive swarms of alate Formicidae, notably *Solenopsis invicta* Buren. The seasonality of prey sizes and abundances was reflected in the distribution of prey caught in the webs of early and late instar colonies (Fig. 2).

No direct effects of meteorological conditions on the rhythmic behaviour of the colonies were found (Fig. 3). Although the number of spiders active varied from day to day, changes in activity could not be correlated with weather. Spiders were even observed active during rains, when there was very little insect activity.

Conspecific interactions

Although some aspects of the social behaviour have already been discussed, during the nocturnal phase behaviour is largely solitary. Fidelity for web sites was not found (Fig. 4). Marked spiders were found to spin webs preferentially in the same general area as the previous day, but this preference declined significantly with time ($r = 0.703$; $P < 0.05$), as spiders migrated to other parts of the communal capture web to spin their own individual orbs.

As for web site fidelity, individual spacing was also found to vary with time. Individual distances increased over time, markedly so after moults (Fig. 5). The lower values of the distance between web and spider and of individual orb web diameters after moulting may be attributed to the larger number of spiders that did not spin orbs during the pre-moult period. A minimum of 15 days intervened between the construction of the last orb and the final moult to adult (Fig. 5).

During all observations in the field, no cannibalism was detected. Moreover, spiders taken from one colony and transferred to another were not attacked by their new colony mates, nor was escape behaviour observed. When collecting incipient colonies in the field, the disturbed spiderlings would drop into the lower herbaceous vegetation where they would immediately aggregate. If left unmolested, they would rejoin the undisturbed portion of the colony by the silk lines they spun while escaping. However, on the ground, the spiderlings were quickly found and attacked by ants (*Pheidole oxyops* and *Solenopsis invicta*). Juvenile colonies would return to the original daytime retreat when displaced to distances of up to 10 m from the retreat.

Population phenomena

E. bistriata was apparently univoltine in Paraguay.

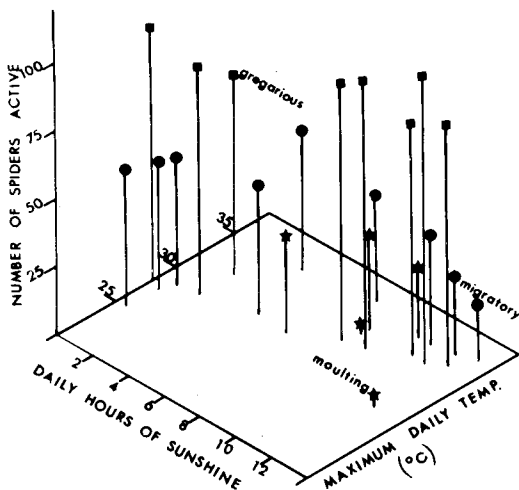


Fig. 3: Environmental factors as related to spider activity during the nocturnal active phase. N = 22.

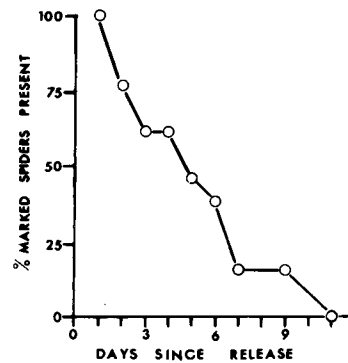


Fig. 4: Temporal fidelity for individual orb web site selection in field colonies of *E. bistriata*, as determined from marking experiments.

As summer ended, a discernible drop in colony populations occurred, especially after the dispersal of the females following the final moult (Fig. 6). Female dispersal varied over time with respect to rate and heterogeneity (Table 3). Although spiders were not marked, the dispersal values found would be expected of marked individuals, and practically all the females were found. As the values of the rate of dispersal (Table 3) ceased to increase after 5 March 1976, it was assumed that dispersal ended on that date. Later values of the rate of dispersal probably reflected trivial, non-dispersal movements. Heterogeneity with

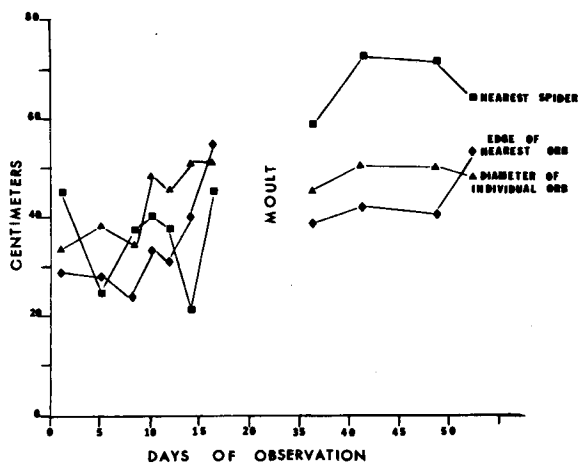


Fig. 5: Changes in individual orb web diameter and individual spacing before and after the last moult to adult in field colonies of *E. bistriata*.

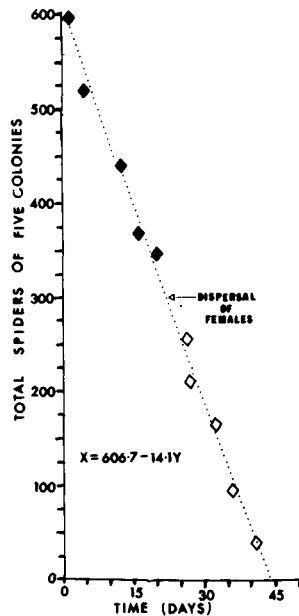


Fig. 6: Dispersal of adult *E. bistrriata* from field colonies. Closed = pre-dispersal phase; open = female dispersal phase.

respect to distance travelled showed a significant departure from normal kurtosis on 29 February 1976, and continued throughout subsequent observations (Table 3).

On 9 March 1976, no solitary males were found, but 12.75% of the females were found, 6.38% of them with males. If the remaining adults can be assumed to have died and if the original sex ratio was equality, there was then an accumulated mortality of 93.22% for both sexes combined (87.25% for females). After 5 March 1976, no additional adults were found alive.

Date	Rate of Dispersal (Clark, 1962)	Heterogeneity of dispersal (Dobzhansky & Wright, 1943)	P
9 February 1976	84.58	2.836	n.s.
20 February 1976	69.67	3.348	n.s.
29 February 1976	93.69	2.601	0.01
5 March 1976	117.29	2.544	0.01
7 March 1976	116.72	2.403	0.01
9 March 1976	114.28	2.526	0.01

Table 3: Dispersal parameters of adult female *E. bistrriata* in an urban area of Central Paraguay.

Clutch size	Number of clutches	Frequency of occurrence
400-449	1	0.0256
450-499	9	0.2308
500-549	9	0.2308
550-599	12	0.3077
600-649	6	0.1538
650-699	2	0.0513
Totals:	39	1.0000

Table 4: Field clutch sizes and frequencies of *E. bistrriata* in one 480,000 m² plot in Central Paraguay.

Spiderlings emerged from 4 May 1976 until 17 May 1976, from cocoons deposited by the females after dispersal. As these cocoons were left in the last site where a female was observed, an estimated hatching success of 40.62% (39/96) was estimated for the cocoons. Mean clutch size was 551.5 ($S^2 = 126.47$) (Table 4). Incipient colonies had a much higher population than pre-dispersal, adult colonies ($x = 131.4$, $S^2 = 96.98$). These differences were significant ($t = 5.98$, $P < 0.001$). The density of pre-dispersal, adult colonies was 5/480,000 m² (= 0.104/ha), while that of incipient colonies was 39/480,000 m² (= 0.812/ha). The net reproductive rate of the colonies in the habitat, calculated from these data, was thus $R_0 = 32.74$.

Instar numbers and synchrony

Eight post-embryonic instars were found in laboratory colonies of *E. bistrriata* (Fig. 7). However, it is not certain whether this number is a product of laboratory manipulation, or is natural, as minor morphological differences were found between laboratory and field reared individuals. Growth patterns followed a geometric pattern (Fig. 7).

Through the first 5 post-embryonic moults of laboratory colonies, synchrony was quite marked (Fig. 8). After the moult of the first spider, the remainder of the cohort moulted within one week. However, as approximately 5% of the cohort was cannibalized during each moulting period, those data given in Fig. 8 denote the surviving cohort. It is likewise uncertain if cannibalism was a product of laboratory manipulation. Moreover, after the first 5 post-embryonic moults, the colonies did not show

further nocturnal clumping, contrasting drastically with field colonies. This may have been a product of space limitations.

Discussion

The results of these observations confirm many of the observations of early naturalists. The nest structure of the colonies coincided basically with the descriptions of Azara (1809) and Masterman (1891). Activity cycles were as described by Masterman (1869). The activity cycles of incipient colonies may be a physiological adaptation to lower nocturnal temperatures. If *E. bistrriata* evolved in the Gran Chaco Basin, where xeric conditions predominate, nocturnal web construction and prey capture would correspond with higher nocturnal relative humidities, while the daytime clumping would occur during lower daytime relative humidities. Metabolic rates would be higher at night, and lower during the day when transpiration could be critical (Anderson, 1970). The clumping would also serve to minimize transpirational water loss. Furthermore, as Horn (1968) has shown for birds, colonial roosting and nesting should occur theoretically when food shows patchiness in time or space. Wilson (1975) further notes that communal clumping or roosting does not preclude the establishment of 'microterritories', or the orbs of *E. bistrriata*. Wilson (1975) also states that the group would be concentrated to forage as a unit, and, thus, spiders would be available to capture larger prey.

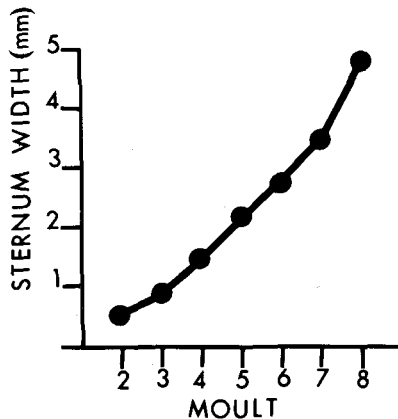


Fig. 7: Mean growth pattern of post-embryonic instars of female *E. bistrriata* in laboratory colonies. N varied from 46 to 10.

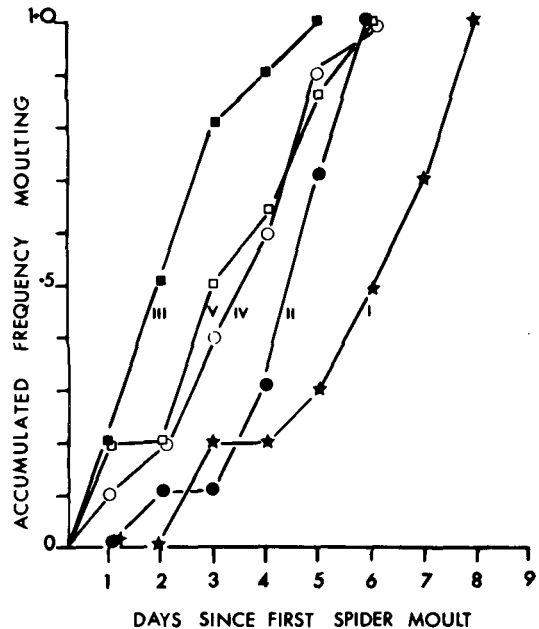


Fig. 8: Synchrony in moulting of laboratory cohorts of *E. bistrriata* after the first spider had moulted. Some cannibalism occurred, and the accumulated frequency moulting refers to the surviving cohort. N varied from 46 to 10.

The adaptive functions of the observed activity rhythms may reside in the avoidance of harsh physical factors (Cloudsley-Thompson, 1960). This adaptive function would also probably hold for potential prey, and thus the active phase of prey capture would also correspond with the greatest amount of insect activity. However, the constant weaving and re-collection of individual orbs must entail a tremendous amount of energetic expenditure, which must be compensated for by prey capture.

Individual orb web diameter increased after moults, which was to be expected (Witt & Baum, 1960). Individual distance also increased following moults, although the maximum distance observed between spiders during the study was much less than the 2 m estimated by Darwin (1845). Orb web diameters were also much less than the 1 m reported by Mello-Leitão (1932), but total web extension of 30 m or more corresponded with previous observations (Azara, 1809).

The prey observed during this study were similar to those described by Azara (1809), who mentioned

their role as predators of reproductive ants. However, unlike Masterman (1891), no rejection of small prey was observed, but rather it was consumed at dawn when the web was gathered in. One long-horned grasshopper (Tettigoniidae) was, however, cut free of an orb and dropped to the ground, but this was the only case of prey rejection observed. Communal feeding has previously been reported for *E. bistrata* by Rengger (1835), Masterman (1869), Azara (1809), and Goldi (1892), although no relations were drawn with respect to communal feeding as a function of prey size. Prey, whose size would be prohibitive for capture by solitary individuals, are capable of being utilized through co-operative effort. The colonial orb weaving *Metabus gravidus* does not exhibit co-operative prey capture tactics (Buskirk, 1975a). Moreover, as practically all prey is large relative to the size of early instar spiders, communal prey capture and feeding probably also serves to increase survival at this stage of development, especially since maternal care is non-existent.

Changes in the location of individual orbs from day to day, as is also found in *M. gravidus* (Buskirk, 1975a), cannot easily be explained owing to the fact that these changes are not random, but increase over time. As satiation reduces the frequency of web construction (Witt, Reed & Peakall, 1968), it would appear that for a particular region of the communal capture web the predictability of prey capture is time dependent. This aspect may be of importance in explaining the synchronous development of the spiders within the colony.

Although cannibalism was observed in the laboratory (5% per moult), it is uncertain if this was a result of the laboratory conditions, or reflected the true behaviour of *E. bistrata*, as cannibalism was never observed in the field. As all laboratory cannibalism occurred during moulting, if it does occur naturally it could account for some of the discrepancy in population size found between incipient and pre-dispersal, mature colonies. Individual body size increments apparently also follow Dyar's constant, as a geometric progression was approximated in the development of laboratory individuals.

As moulting was highly synchronised within a colony, but loosely synchronised between colonies, the best explanation of this phenomenon would tentatively be that during the daytime clumping

either a contact pheromone, or the presence of moulting hormone in the cuticle of recently moulted or ready to moult individuals, stimulates others to gear their physiology to moult. We know of no other literature on Insecta or Arachnida which addresses this question. Developmental synchrony also fits in nicely with a proposed step in the evolution of invertebrate, coloniality through the physiological and behavioural integration of the individuals of the colony (Beklemishev, 1969).

Field populations showed significant differences between mature and incipient colonies, indicating that either colonies divide before maturing, or that there are factors, possibly unobserved cannibalism, which produce a high mortality. From the colony densities, it would appear that the latter is probably the case. As the mature females are approximately 2.5 cm long, the clutch sizes are about one half those of solitary orb weavers, as estimated from the regression equations of Enders (1976). This suggests that communal life may increase survivorship, and thus warrant a lower than expected fecundity. Also, as Williams (1975) has pointed out, larger organisms generally have lower mortality rates than smaller ones. Nevertheless, the discrepancy between juvenile and adult populations would tend to indicate that there is a high degree of mortality during maturity, and reaching a large size, at which mortality would be reduced, may be important.

Rengger (1835) reported colony populations of 30-40, Azara (1809) of less than 100, and Masterman (1869) of over 300. The data presented here indicate that populations tend to vary in size over time and generation. The earlier reports on populations may have been taken at different times of colony development, or may have been taken from quite different habitats. Although no inter-colonial migration was observed, it is possible that colonies could fuse to exploit limited nesting sites, such as those of isolated trees in the more xeric portions of the Chaco. Acceptance of spiders from other colonies during this study would tend to indicate support for this possibility. Further studies are necessary to determine the causative factors of these temporal, and perhaps spatial, changes in populations.

Although spiders are generally considered the typical solitary animal, different degrees of social behaviour have been documented for many species

(Kullmann, 1968, 1972; Shear, 1970). Kullmann (1968) recognized three characteristics necessary for sociality in spiders: (1) mutual aggressiveness must be minimized and mutual tolerance maximized; (2) there must be mutual attraction between individuals; and (3) individuals must exhibit co-operative behaviour. Shear (1970) speculates that sociality in spiders (1) increases the efficiency of prey capture, (2) provides additional protection from parasites and predators, and (3) promotes increased parental investment in the progeny. He also points out that the web was one of the essential pre-adaptations for spider sociality.

E. bistriata does not easily fit into the existing schemes of classification of spider sociality (Kullmann, 1968; Shear, 1970; Wilson, 1971). *E. bistriata* would correspond to the subsocial of Kullmann (1968), the semisocial of Shear (1970), and high in Wilson's (1971) evolutionary pathway. Although there is no overlap of generations, *E. bistriata* does exhibit co-operative prey capture and communal feeding, and consequently poses a problem in classification. *E. bistriata* apparently possesses the most advanced form of sociality yet described for orb weavers. Although *Metabus gravidus* shows overlapping generations, it is much less co-operative, and shows a high degree of cannibalism (Buskirk, 1975a, 1975b). Likewise, *E. bistriata* far outdistances the social level achieved by *Cyrtophora citricola*, as described by Lubin (1974). However, its social behaviour is not as advanced as that of the cribellate sheet web spinners *Stegodyphus sarasinorum* (Kullmann, 1969; Bradoo, 1972), *Anelosimus eximius* (Simon, 1891; Comstock, 1948; Brach, 1975), *Agelena consociata* (Krafft, 1971, 1975) and *Mallos gregalis* (Burgess, 1976), all of which exhibit co-operative prey capture and feeding, have overlapping generations, and show some degree of care of the young. However, the cribellate *E. bistriata* with univoltine, synchronously developing colonies, and adaptive communal prey capture and feeding may benefit most from its developmental coloniality, apparently through the exploitation of otherwise non-exploitable flight lanes and large prey, and perhaps through increasing individual survivorship associated with its large size.

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