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POPULATION STRUCTURE IN THE SPIDER *ACHAEARANEA TEPIDARIORUM* (ARANEAE, THERIDIIDAE)[1]

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ABSTRACT

Two distinct types of population structure are present in the spider *Achaearanea tepidariorum*, each with totally different dynamics and behavior.

The *floating population* or dispersion stage is composed entirely of second instar spiderlings, representing about 99 per cent of the total produced by the species. This population is characterized by a very diverse genetic composition and a high mortality. Several different strategies are observed in spiders in general to reduce mortality in the second instar.

The *established population* is composed of individuals with snaring webs and sedentary habits, and begins as an immature population after the invasion of an available habitat by the second instar. During this phase, its numbers increase first at the maximum intrinsic rate until the maximum habitat capacity has been reached. In a mature population more than 65 per cent of the biomass is contributed by the adult individuals.

INTRODUCTION

Although spiders are among the most diversified groups of animals and many species are locally very abundant, a review of the literature shows little work done on their population biology (Turnbull, 1973).

Two distinct types of population structures are present in many spider species, each with different characteristics regarding dynamics and behavior: the floating population and the established population.

The characteristic aeronautic behavior (ballooning) is the means of dispersion in most spider species. Small species can balloon during any instar, even as adults (Duffey, 1956). In medium to large sized species, effective dispersal by ballooning is probably restricted to the second instar, since small body size seems an important factor for a long distance dispersing mechanism. Large orb-weavers and wolf spiders are sometimes lifted by the wind (J. Anderson and H. K. Wallace, 1973, personal communications), but this phenomenon is probably associated with short distance travel.

In general, aeronautic behavior is dependent upon wind currents of specific velocity and direction (Ritcher, 1967).

In *Achaearanea tepidariorum* (Theridiidae) air currents have a definite effect on basic behavioral patterns (Turnbull, 1964), and in long distance travel and dispersion ballooning spiderlings can resist starvation for 25 days or longer (Valerio, 1975a), which implies a mixing of individuals from different populations. Obtaining food by trapping has severe limitations in the second instar. In general these spiderlings are unable to catch

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anything larger than their own size (Ewing, 1918) and survival is very low (less than 2 per cent, Valerio, 1975a). In some related species, regurgitation by the mother is an effective mechanism to transfer energy to the second instars (Kullmann, 1969), but it has been shown that regurgitation does not occur in *A. tepidariorum* (Kullmann and Kloft, 1968). This species provides inviable eggs to feed the spiderlings inside the sac (Valerio, 1974).

The present report intends to further the understanding of these aspects and the structure of the established population.

MATERIALS AND METHODS

Three populations of spiders (each from a different building) on the Universidad de Costa Rica main campus were selected for study. All individuals with an established web and all fresh egg sacs were collected by hand and preserved in alcohol for later analysis. The length of the carapace easily separated the several immature instars except for the sixth and seventh, collectively called subadults (some males reach maturity at the sixth instar, Bonnet, 1935).

The number of ballooning spiderlings of these three established populations was estimated taking into consideration the survival in this instar as shown by data from observations under controlled conditions (Valerio, 1975a). Mortality in the first instar was considered negligible for statistical purposes (2,642 of 2,683 nymphs under observation molted to the second instar, that is, 98.47 per cent survivorship).

Several cohorts of spiderlings (i.e., siblings emerging from the same egg sac) were kept in covered glass jars and checked daily to record the mortality rate.

RESULTS AND CONCLUSIONS

Floating Population.—This population is composed entirely of second-instar spiderlings, representing about 99 per cent of the total emerging population (Table 1).

After hatching the spiderlings remain inside the egg sac for four days, feeding on undeveloped eggs (Valerio, 1974), and upon emergence, they aggregate in a dense clump near the sac. Later they become progressively more active, build a communal web in the center of the maternal web and commence dispersion. By the tenth day they have all left the web.

Two mortality peaks are observed in unfed second instar spiderlings, one during the gregarious phase near the egg sac and the other, 13-14 days after ecdysis (long after dispersion has begun). Cannibalism never develops in this instar; the spiderlings make no attempt to attack each other, nor do they feed on the dying mates (except when attacked by a certain parasitic microhymenopteran, Valerio, 1975a).

Established Population.—This population includes individuals from all active instars and the adults of both sexes. Sedentary habits and trapping webs are characteristic at this stage.

Newly available habitats are invaded by second instar spiderlings from the floating population. During the period of invasion, interspecific competition is very strong. For instance, in Costa Rica, spiderlings of ten different species can become established in human dwellings.

With every molt, the spiderlings required a larger web area, which enhances intraspecific competition, and consequently, the number of individuals in the population is reduced. However, the biomass increases as the number of individuals decreases (Fig. 1),

Table 1.–Population composition in *Achaearanea tepidariorum* (Pooled data from three natural populations).

Instar	Number of individuals	Percentage of individuals	Biomass (a) in mg	Percentage of biomass
Eggs (b)	14032	(37.35)	2.0759	(27.83)
First	13137	(35.20)	1.5985	(21.43)
Second**	9791	(26.25)	0.8765	(11.75)
Second*	127	(0.34)	0.1016	(1.36)
Third	93	(0.26)	0.2339	(3.14)
Fourth	43	(0.12)	0.2675	(3.59)
Fifth	21	(0.06)	0.2192	(2.94)
Subadult	15	(0.05)	0.1911	(2.56)
Males	15	(0.05)	0.1049	(1.42)
Females	113	(0.32)	1.7888	(23.98)
TOTAL	37387	100.00	7.4579	100.00

* Individuals with established webs.

** Floating population, calculated on the basis of 76.67 survivorship in second instar up to dispersal. (Valerio, 1975a)

a) Biomass according to Table 2.

b) From 63 egg sacs.

which implies more biomass per unit volume with every molt.

The webs seem to have minimum size requirements and neighboring webs do not normally overlap at any point. An enclosure measuring 1200 cm^3, appropriate for one fourth instar spider that weights about 62 x 10^{-4} mg (Table 2), proved too small for more than one third instar spider (25 x 10^{-4} mg) and at most two second instar spiderlings (16 x 10^{-4} mg) may survive in it. The spiders did not seem able to capture prey, even when abundant, without an established web.

A growing population probably attains its maximum size before the spiders reach maturity. However, in a mature population a large proportion of the individuals are adults (30 per cent) contributing 65 per cent of the total biomass (Fig. 1). The remaining 35 per cent of the biomass is composed of the six active immature instars.

The individuals in the aerial population may come from distant geographical areas and thus a very diverse genetic composition is probably involved.

The first mortality peak (during the gregarious phase) is probably due to anatomical or physical defects. The second peak (13-14 days after ecdysis) is due to starvation in unfed spiderlings.

Some species provide inviable eggs to feed the spiderlings inside the sac. In *A. tepidariorum* and related species the first instar is of short duration and feeding does not take place until the second instar (Valerio, 1974).

Natural selection would be predicted to favor a tendency to have a larger portion of inviable eggs instead of producing unadapted individuals. This strategy would reduce the mortality during the gregarious phase and provide more food for the surviving individuals, thus reducing also the second mortality peak.

Another possible way to reduce this mortality would be through cannibalism so that the portion dying during the gregarious phase would be "harvested" by the stronger

Table 2.–Body weight in *Achaearanea tepidariorum*

Instar	Fresh weight in mg ($X10^{-4}$)
Egg	1.36
First	1.37
Second	8.00
Third	25.16
Fourth	62.22
Fifth	104.38
Sixth and Seventh*	127.41
Adult female	158.30
Adult male	69.92

* Subadults

individuals. In this way the mortality due to starvation would be reduced. This system represents the optimal tactic for a predator (Slobodkin, 1968).

In some species, cannibalism is believed to be the usual and even sole means of survival (Gertsch, 1949) and probably plays an early role as a primitive condition in the evolution of the other advanced behavioral mechanisms.

Maternal care is another evolutionary strategy toward a more effective means of survival. This condition implies the gradual loss of aggressivity by the mother. Some spiderlings use the food left over by the mother (Darchen, 1965), while others feed on freshly captured prey simultaneously with the parental female as commensals (Darchen, 1965, 1968), or on prey specially captured by the mother for this purpose (Kullmann, 1970). A culmination of this evolutionary line is the feeding of the young by regurgitation (Kullmann and Klot, 1968), reinforced under extreme conditions by the sacrifice of the mother as food for her offspring (Kullmann, 1969).

Summarizing, the second instar is of critical importance for the species, since it is the dispersing stage. But high mortality of these aeronautic individuals makes this instar very expensive for the bioeconomy of the species.

It is postulated, then, that selective pressure favors those mechanisms tending to liberate the second instar from feeding on external prey sources. After the second instar he spiderlings gain in size and aggressivity, and prey capturing does not seem to be a problem anymore.

The available habitats are invaded by spiderlings from the floating population. The number of invaders that become established seems to depend directly on the availability of web-building sites, which indicates a strong interspecific competition during this period. Other factors being equal, the species with the largest initial number of immigrating individuals has the highest probability to exclude its direct competitors, hence the critical importance of large floating populations.

When an established spiderling increases in size (i.e., through growth and molting) it requires a larger web area, which stimulates intraspecific competition and reduction in number of individuals. However, it seems that the relative increase in hunting area is smaller than relative gain in body weight, which implies more biomass per unit area with

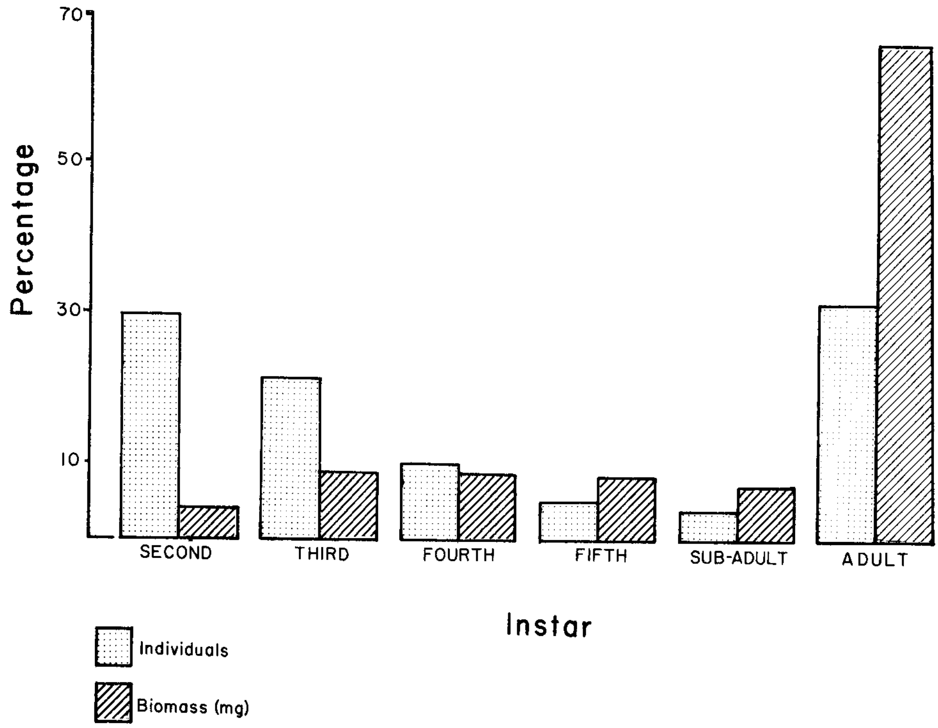

Fig. 1.–Composition of a natural population of *Achaearanea tepidariorum*. Data from Table 1, only individuals with an established web were computed.

every molt. Thus, as individuals increase in size the population more completely exploits its environment.

Since adult females are the largest individuals in the population (Table 2), natural selection would favor this system in which the established population is composed mainly of adult females.

During the growth following invasion the population probably increases at the maximum intrinsic rate. This exponential growth is easily understood because the natural rate of increase is independent from the density since adult spiders are not present during the growing phase. The population size is then maintained at a very stable level (Valerio, 1975b), varying only with the normal fluctuations in environmental conditions.

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