

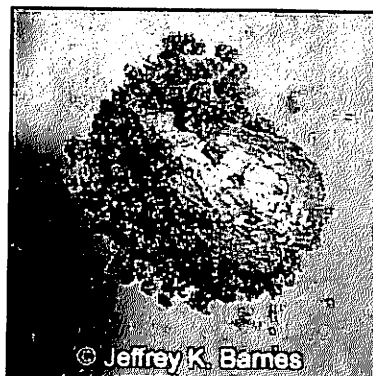
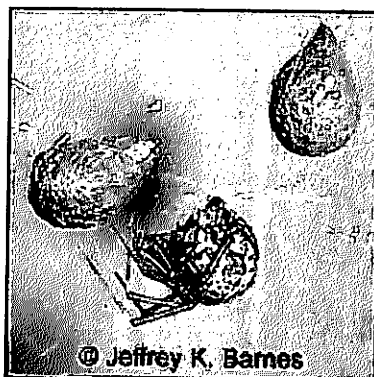
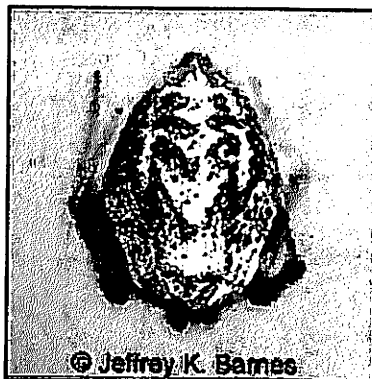
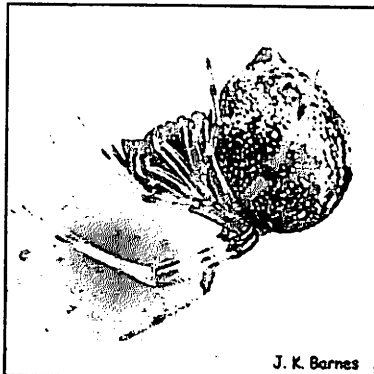
Number 17 • May 9, 2003 • Jeffrey K. Barnes

Common house spider

Order: Araneae

Family: Theridiidae

Genus and species: *Achaearanea tepidariorum* (C. L. Koch)



This very common household spider would be inconspicuous if it were not for its persistent and unseemly webs. Many of the dusty cobwebs hanging from corners of neglected ceilings are remnants of this species' work. The body of the female is up to ¼ inch in length; that of the male is considerably smaller. The cephalothorax is brown dusted with black. The white or light yellow legs have brown and gray apical annulations on most segments, and there are additional annulations at midlength on the first and second pairs of tibiae. The abdomen of the female is high and inflated, and near its highest point posteriorly there is a dark spot surrounded by light and dark U- or V-shaped markings. The abdomen is otherwise light tan and gray with white speckles.

This species has a cosmopolitan distribution and has probably been transported around the world by man. It is abundant in the United States, Mexico, and Central America, and it may be native to South America (Levi 1963). Individuals live a year or more and adults are found in all seasons. This species is rarely found in natural communities except for caves and dry, overhanging rock ledges (Beck and Dorris 1982, Hodge and Storfer-Isser 1997; McDaniel et al. 1979). It is found in many kinds of artificial communities, such as fields and roadsides, farmyards, gardens, vacant lots, cemeteries, and man-made structures (Archer 1946). It is a common and characteristic species of houses, barns, and sheds, often found near outdoor light fixtures. Indoors, house spiders are most likely to be found in humid areas such as basements, crawlspaces, and porches.

The irregular, tangled cobwebs are typically hung in situations that afford overhead shelter. The spider often rests in a retreat within the web. Sites for webs are chosen randomly. Webs that do not yield adequate prey are soon abandoned, and these become littered with dust and debris. Suitable sites with plentiful prey are systematically filled with webbing (Turnbull 1964). Spiders often build webs in areas to which air currents direct prey. Prey consists chiefly of flying insects and other arthropods, including some that are much larger than the spider. In fact, the common house spider is well known for its ability to overpower relatively large prey. Remains of spider wasps, large flies, such as calliphorids and tabanids, beetles, cockroaches, leafhoppers, and harvestmen have been found under webs (Fitch 1963). The common house spider has even been known to feed upon lone star ticks (Archer 1946, Guarisco 1991) and purseweb spiders (Guarisco 1988).

Common house spiders tend to form aggregated populations. Females typically build webs in close proximity to each other, and webs of different individuals are often attached (Hodge and Storfer-Isser 1997). However, females are incompatible, and if they should come into contact one may become prey to the other. Males and females may share the same web for long periods, hanging upside down from the silken threads. The light brown, pear-shaped eggs sacs are produced from late spring to late summer. They hang freely in the web, and each may contain from 100 to 600 or more eggs (Kaston 1981, Miyashita 1987). The sacs have a tough, papery covering and measure up to ¼ inch or more in diameter. A single female can produce many of them during one season. The first instar spiderlings do not feed. Second instars remain in the sac for several days, feeding on undeveloped eggs. These spiderlings emerge and float away on silken threads caught by air currents (Valerio 1974, 1977). This aeronautic behavior is called ballooning, and it is a characteristic means of dispersion in most spider species. The floating spiderlings establish populations in new habitats.

Rarely have common house spiders been known to bite humans, and their bites apparently do not result in serious symptoms, such as local ulcers, necrosis, or serious systemic symptoms (White et al. 1989).

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FEEDING ON EGGS BY SPIDERLINGS OF *ACHAEARANEA TEPIDARIORUM* (ARANEAE, THERIDIIDAE), AND THE SIGNIFICANCE OF THE QUIESCENT INSTAR IN SPIDERS¹

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ABSTRACT

Feeding on inviable eggs by spiderlings is known to occur in several families. This activity has been observed in the first (quiescent) instar only, leading to the general belief that this first instar always undertakes the utilization of such eggs. However, the present study indicates that egg feeding occurs in the second instar in *Achaearanea tepidariorum* (Theridiidae), with the reduction in time period of the quiescent instar. There seems to be a tendency in the Theridiidae (and, perhaps, in some related families as well) toward the elimination of the quiescent instar. Egg-feeding considerably extends the life span of spiderlings and, sometimes, provides enough nourishment to carry spiderlings to the third instar without additional food intake.

INTRODUCTION

It should be readily apparent to arachnologists that, in many cases, some of the spiderlings emerging from an egg sac are heavier than the rest, having a more bulky abdomen. This condition is correlated with the presence of dried eggs inside the sac. The consumption of unfertilized (or otherwise inviable) eggs is known to occur in several families of spiders (Lecaillon, 1904; Holm, 1940; Schick, 1972), although seldom observed and photographed (Peck and Whitcomb, 1970). This feeding activity has been directly observed only in the first instar (i.e., before the first true molt), leading many workers to suppose that egg-feeding takes place only in this instar. However, the data herein reported on *Achaearanea tepidariorum* (C. L. Koch) reveal the presence of a different strategy.

MATERIALS AND METHODS

Several adult female spiders were kept under controlled conditions to provide fresh eggs of known age. Egg sacs were separated from the maternal web and kept in a constant temperature ($24.5 \pm 0.3^{\circ}\text{C}$) cabinet. Some hatched spiderlings were individually isolated in vials before the first true molt (i.e., while in the first instar). Others were permitted to molt and emerge from the sac, and then were isolated. These two groups of

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spiderlings were kept without food to measure their survival capacity. The vials were checked daily and the number of dead spiderlings recorded. Groups of eggs were checked daily under the dissecting microscope to study morphological changes related to reversion, rupture of chorion and first molt. Some eggs were submerged in paraffin oil according to the method of Holm (1940) to render the chorion transparent so that the embryo could be observed.

RESULTS AND COMMENTS

In the group of spiderlings isolated before the first molt, all individuals had died by the 23rd day. In the group of individuals isolated after emergence from the egg sac, (thus, after the first molt), about 25% survived beyond the 23rd day (Fig. 1). Furthermore, over 3% of these spiderlings molted to the third instar (Table 1).

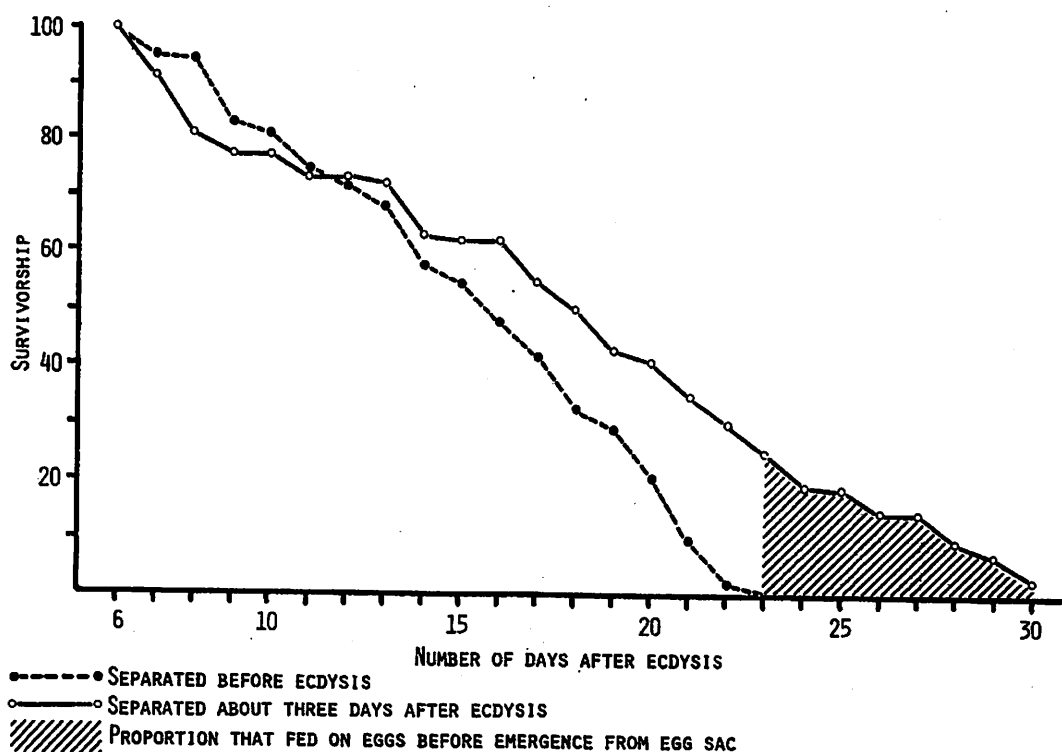


Fig. 1.—Survival in unfed spiderlings of *Achaeareanea tepidariorum* kept individually isolated.

Early Development—During their development, all spiders pass through one or more quiescent stages immediately following eclosion. A variety of names has been applied to these stages in the literature: incomplete stadia (Holm, 1940), nymphs (Vachon, 1953) and deutova (Gertsch, 1949), among others. Many embryonic characteristics are retained, e.g., lack of segmentation in the appendages and traces of abdominal segmentation in some species. Hairs and pigmentation are absent, and motility is very poorly coordinated.

In species with more than one such stages, feeding on inviable eggs seems to be a widespread phenomenon in the families Scytodidae (Hite, et al., 1966; Galiano, 1967), Clubionidae (Lecaillon, 1904; Peck and Whitcomb, 1970), Gnaphosidae (Holm, 1940) and Thomisidae (Schick, 1972). However, species with only one quiescent stage of short

Table 1.—Survival in unfed spiderlings (*Achaearana tepidariorum*) kept individually isolated (¹ molted to third instar).

Day after ecdysis	Isolated immediately after emergence from egg sac		Isolated just before ecdysis (or during the process)	
	Numbers	Percentage	Numbers	Percentage
6	90	100.00	77	100.00
7	82	91.11	74	96.10
8	73	81.11	73	94.80
9	69	76.67	64	83.12
10	60	76.67	62	80.50
11	66	73.33	58	75.33
12	66	73.33	56	72.73
13	65	72.22	52	67.53
14	57	63.33	45	58.40
15	56	62.22	43	55.84
16	56	62.22	37	48.05
17	50	55.56	33	42.86
18	45	50.00	26	33.77
19	39	43.33	22	28.57
20	37	41.11	16	20.78
21	31	34.45	8	10.39
22	27	30.00	2	2.60
23	22	24.45	0	—
24	17	18.89		
25	16	17.78		
26	13	14.45		
27	13	14.45		
28	8	8.89		
29	5	6.67		
30	3 ¹	3.33		

duration, like *A. tepidariorum* and possibly all theridiids, have their digestive tracts still full with yolk (Dawydoff, 1949) and feeding is unlikely to occur, if in fact it is not impossible. This assumption is further supported by the particularly feeble and uncoordinated movements in this second group. Yet survival in this stage in *A. tepidariorum* is very high (98.46% in laboratory rearings).

Several literature reports on feeding by this stage in the family Theridiidae (Juberthie, 1957; Bouillon, 1957; Kaston, 1970) appear to be the result of incomplete observations. Feeding does occur inside the egg sac by the second-instar spiderlings, as is reported herein (see below) but not by the quiescent instar. Information on related families is completely lacking.

Adaptative value of this first instar has been questioned by Gertsch (1949), since it represents an unnecessary exposure with apparently no adaptive gain (the stage could have been passed inside the egg). This situation is comparable to the life cycle of insects with complete metamorphosis, in which a quiescent stage also occurs (pupa). But in the latter case the pupa follows active feeding instars, and provides a protective structure for important physiological and morphological changes. It has been suggested by Schick (1972) that the sole function of quiescent stages in spiders is to allow feeding on inviable eggs, to produce stronger spiderlings in the next instar. This latter hypothesis seems tenable where the phenomenon is known to occur. In theridiids, however, and perhaps in

other related families, there is an associated tendency for temporal reduction of the quiescent instar.

Nomenclatural Systems—Presently used terminology for different stages in the development of spiders is chaotic. Some workers seem to ignore or misunderstand terms used by previous investigators. In other cases, apparent conflicts between systems are just the effect of differences among the species under study. For instance, the phenomenon of "reversion" is considered a basic turning point in some systems, and totally ignored by others.

After analysis of the literature and comparisons among the main systems and opinions, I have concluded that all developmental sequences can be grouped into three nomenclatural categories. This division is based on two simple characteristics: 1) Reversion or eclosion can be considered the end of the embryonic period; 2) Free hunting stages can be considered totally different or a nomenclatural continuation of quiescent stages (Fig. 2).

The three categories are characterized as follows:

I. The embryonic stage is defined as continuing until eclosion. The same nomenclature is used for the quiescent and active instars. This category includes the ideas of Ewing (1918), Hite, et al. (1966), and Peck and Whitcomb (1970).

II. The embryonic stage is also considered to continue until eclosion. However, a different nomenclature is used for the quiescent and active stages. Authors supporting this system are Holm (1940), Juberthie (1964), Eason and Whitcomb (1965), and Gertsch (1949).

III. The embryonic stage is considered to end with reversion. A different nomenclature is used for the quiescent and active instars. This system was basically developed by Vachon (1953, 1957) and was followed or modified by Galiano (1967, 1969) and Schick (1972).

Reversion (from the German *umrollung*; *inversion* in French and Spanish) is, basically, the moving of the ventral structures derived from the germ layer to a dorsal position (Dawydoff, 1949). It is exclusively characteristic of arachnids, and well studied in the Araneae by embryologists, although largely overlooked or totally ignored by workers doing life history studies.

In *A. tepidariorum* reversion is completed by the fifth day (at 217 hours, according to Montgomery, 1909). As a result of reversion and of developmental changes associated with it, the exuvial liquid is absorbed by the embryo and then the chorion outlines the body and the appendages. This new appearance is easily detected, even with the naked eye.

Four days after reversion, eclosion occurs (i.e., shedding of the chorion and vitelline membrane, simultaneously in this species). The stage resulting after eclosion is then not enveloped in any membrane and molts directly into the active instar. The egg teeth were not observed, but the egg inclosure ruptures along the anterior margin of the clypeus.

Duration of the First Instar—The first instar is composed, then, of a single stage of a two-day duration. Almost half of the duration of this quiescent instar is actually the pharate second instar. That is, the second instar is anatomically achieved (apolysis) some 30 hours after eclosion, but the old skin is not shed (ecdysis) until some 18 hours later. The nomenclature here follows Jenkin (1966) and Jenkin and Hinton (1966). The hairs and well-pigmented eyes of this pharate second instar can be easily seen through the first instar skin.

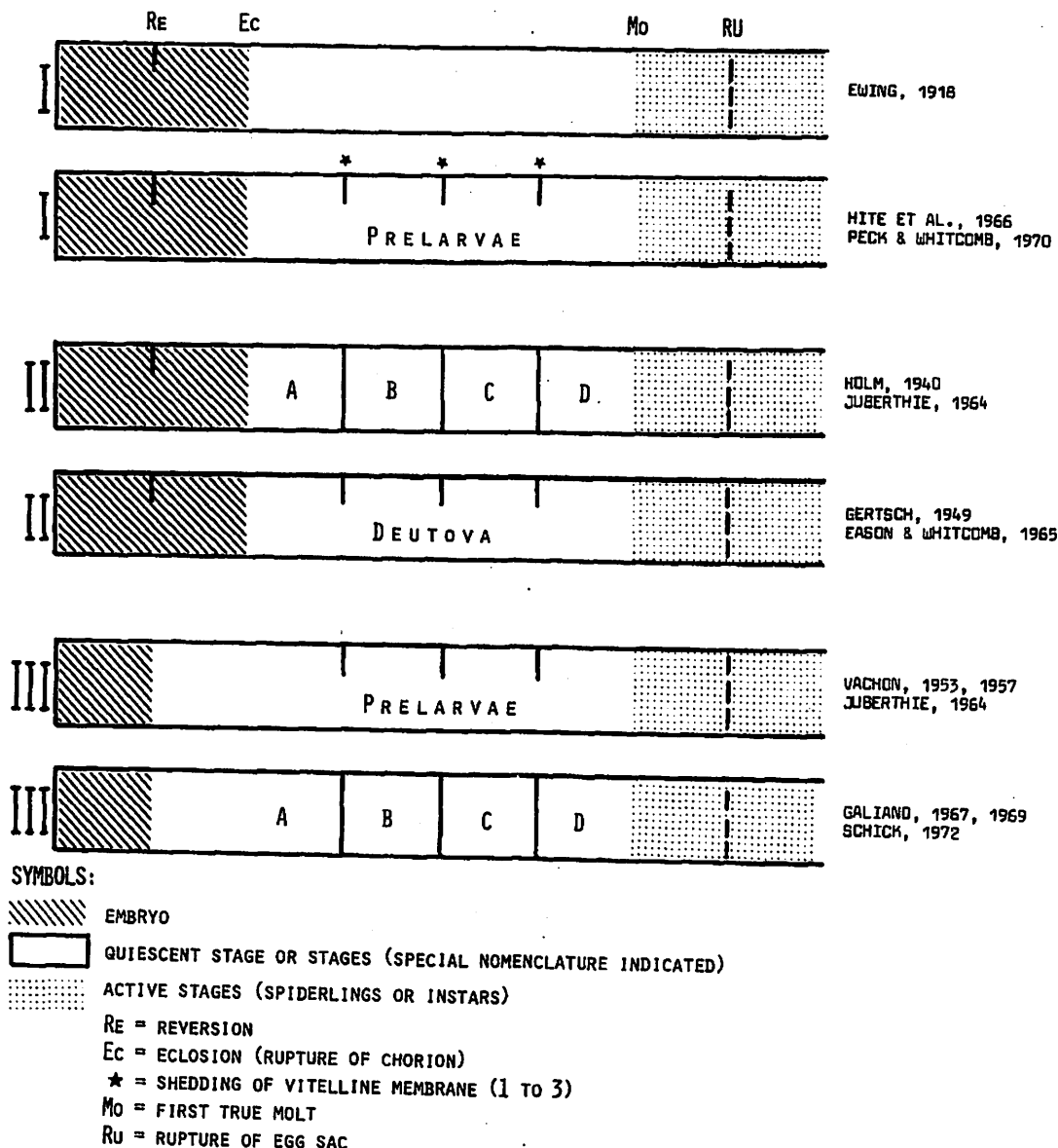


Fig. 2.—Principal nomenclatural systems in spider embryology and early development.

Feeding—After ecdysis the first active spiderlings (second instar) remains inside the egg sac for four days, a period during which the spiderlings normally feed on eggs that did not complete development. This period seems to vary with ambient temperature and other ecological factors such as wind and humidity; after which one or sometimes two holes are cut in the sac wall, and the spiderlings emerge. When a large number of inviable eggs are available and few spiderlings develop they molt to the next instar without any additional food intake (Table 1, 30th day).

CONCLUSIONS

Very short duration of the quiescent period (i.e., first instar) in this species seems to indicate a trend toward the elimination of this stage in the family Theridiidae and related groups. This elimination would be possible since its presumable function, (Schick, 1972) seems to be taken by the first active instar (second instar) during the period of life within

the egg sac. Utilization of inviable eggs, originally a role for the quiescent instar (1 to 4 stages), seems to be undertaken by the second instar with a consequent temporal reduction of the first instar.

Difference in survival in the two groups of spiderlings is clearly attributed to egg-feeding before abandonment of the egg sac. If such feeding does not take place, the maximum life expectancy for a starving second instar spiderling is 22 days (Table 1). The spiderlings that feed on eggs, even though this feeding may not be sufficient in itself to lead to molting, stand a greater chance for survival since the life span is extended considerably by such early nutritional procurement.

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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 *Achaearana tepidarium* (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.

mgは
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(1.42)

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 cm³, appropriate for one fourth instar spider that weights about 62×10^{-4} mg (Table 2), proved too small for more than one third instar spider (25×10^{-4} mg) and at most two second instar spiderlings (16×10^{-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. tepidarium* 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 ($\times 10^{-4}$)	
Egg	1.36	$\rightarrow 10^{-1} \text{ mg}$
First	1.37	これは 平均
Second	8.00	(池田)
Third	25.16	
Fourth	62.22	
Fifth	104.38	
Sixth and Seventh*	127.41	
Adult female	158.30	$\rightarrow 15.83 \text{ mg}$
Adult male	69.92	$\rightarrow 6.99 \text{ mg}$

* Subadults

(池田)
修正

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 the 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

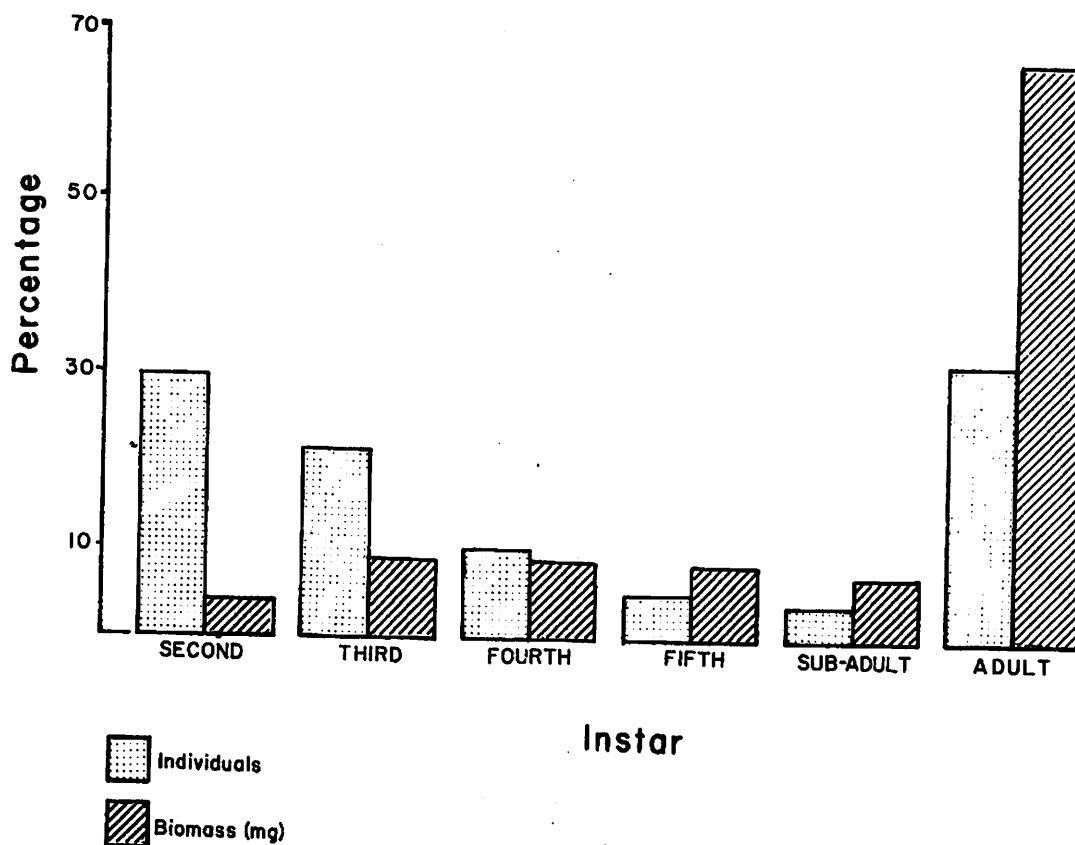


Fig. 1.—Composition of a natural population of *Achaearanea tepidariorum*. Data from Table 1, only individuals with an established web were computed.

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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