

## DEVELOPMENT AND EGG SAC PRODUCTION OF *ACHAEARANEA TEPIDARIORUM* (C. L. KOCH) (ARANEAE, THERIDIIDAE) UNDER LONG AND SHORT PHOTOPERIODS

Kazuyoshi Miyashita

Department of Biology, Faculty of Science,  
Tokyo Metropolitan University, Setagaya-ku,  
Fukazawa 2-1-1, Tokyo 158, Japan

### ABSTRACT

The development and egg sac production of *Achaeearanea tepidariorum* were investigated at 25°C and long (16L-8D) or short (10L-14D) photoperiod. The development of nymphs was completed in 30-80 days in 4-6 molts in the male and in 40-100 days in 5-7 molts in the female. Under the long photoperiod, the development of males was accelerated by the omission of one or two molts when food conditions were favorable, but under the short photoperiod such an acceleration tended to be cancelled by prolongation of either the last instar or the last and penultimate instars. This tendency was also observed in the female, but not so clearly as in the male. The development proceeded more speedily in complete darkness than under light. Adult females produced a mean of 9.7 egg sacs at intervals of 8.1 days. The mean egg number per sac showed a gradual decrease with time. The mean total egg number produced per female was 1812.7, and the mean longevity was 116.5 days in the female and 33.9 days in the male.

### INTRODUCTION

The house spider, *Achaeearanea tepidariorum* (C. L. Koch) is a cosmopolitan species, and quite abundant in many areas. However, studies on the biology and ecology of the spider are unexpectedly few. Although the life history of the spider must have a close connection to the seasonal change of environmental conditions in different localities, there are no detailed analyses on developmental characteristics in relation to the seasonal change in temperature and photoperiod.

In the present paper, I report the results from investigations on the development and egg sac production of the spider under laboratory conditions, with long and short photoperiods.

### MATERIALS AND METHODS

The place where all experimental animals were collected was Abiko City (140°02'E—35°52'N), Chiba Prefecture, Japan.

First-instar spiderlings collected in June, 1984, were reared separately in vials 1.4cm in diameter by 3.0 cm in height. The vial size was increased as the development of each spider proceeded, adults being contained in vials 3.8cm by 10.5cm. In each vial, a strip of thick paper was placed as a substrate.

Spiders were reared at 25°C and long (16L-8D) or short (10L-14D) photoperiod. Light source was a 6w fluorescent tube, which gave 250-300 lux. Relative humidity fluctuated from 55% to 85%.

Rearings were divided into two experiments, A and B, according to the difference in food conditions. In the former, feeding intervals were 3-4 days, but in the latter 2-3 days for first and second instars only. Additionally, two groups were kept at 23°C, one in complete dark except for feeding and vial change, the other under 14L-10D in order to investigate the development under darkness.

Spiders were fed collembolans, mainly *Sinella cuspidatus*, during first and second instars and *Drosophila melanogaster* from third instar to adult. An excess number of collembolans was provided at each feeding. The number of fruit flies provided was changed from one to six following the process of the spiders' development.

The number of individuals used in each experiment varied from 12 to 30. The mortality ranged from 30% to 40% in first and second instars. After this period deaths occurred sporadically due to ecdysis failure.

Wild adult and last-instar females were collected in May 1984, and reared at 25°C and long photoperiod to investigate egg production. Each female was fed a single well-grown larva of *Phaenicia sericata* at the intervals of 3-4 days. Virgin females, except three, were mated with males in the laboratory. The egg sacs produced were removed together with first-instar spiderlings when they had emerged, and the number of spiderlings was counted as an indicator for total eggs since healthy egg sacs rarely contained dead eggs.

## RESULTS

**Effects of photoperiod on development.**—Fig. 1 shows the difference in development of the males reared at 25°C and long or short photoperiod. In experiment A, the development was not significantly affected by photoperiod. The number of days required for the development from first instar to adult was 50-60 days, and the number of molts was five or six.

In experiment B, in which the food regimes during first and second instars were improved, the development was quite accelerated only under the long photoperiod. The development was concluded in 30-40 days, and the number of molts was five, except one individual which molted only four times. Under the short photoperiod, the development required 60-80 days and five or six molts. This difference was mainly due to the prolongation of either the last instar or both the last and penultimate instars. In other words, under the long photoperiod the developmental period becomes short by the omission of one or two molts, if food conditions are favorable. Under the short photoperiod, however, there occurs a tendency to prolong the last instar or both the last and penultimate instars, irrespective of difference in food conditions.

Fig. 2 shows the result for females. The result was essentially the same as the males show in Fig. 1. Developmental acceleration was also observed under the long photoperiod in experiment B. The prolongation of the last instar or both the last and penultimate instars was not clearly observed under the short photoperiod, although one female in experiment B molted seven times and spent more than 40 days in the last instar.

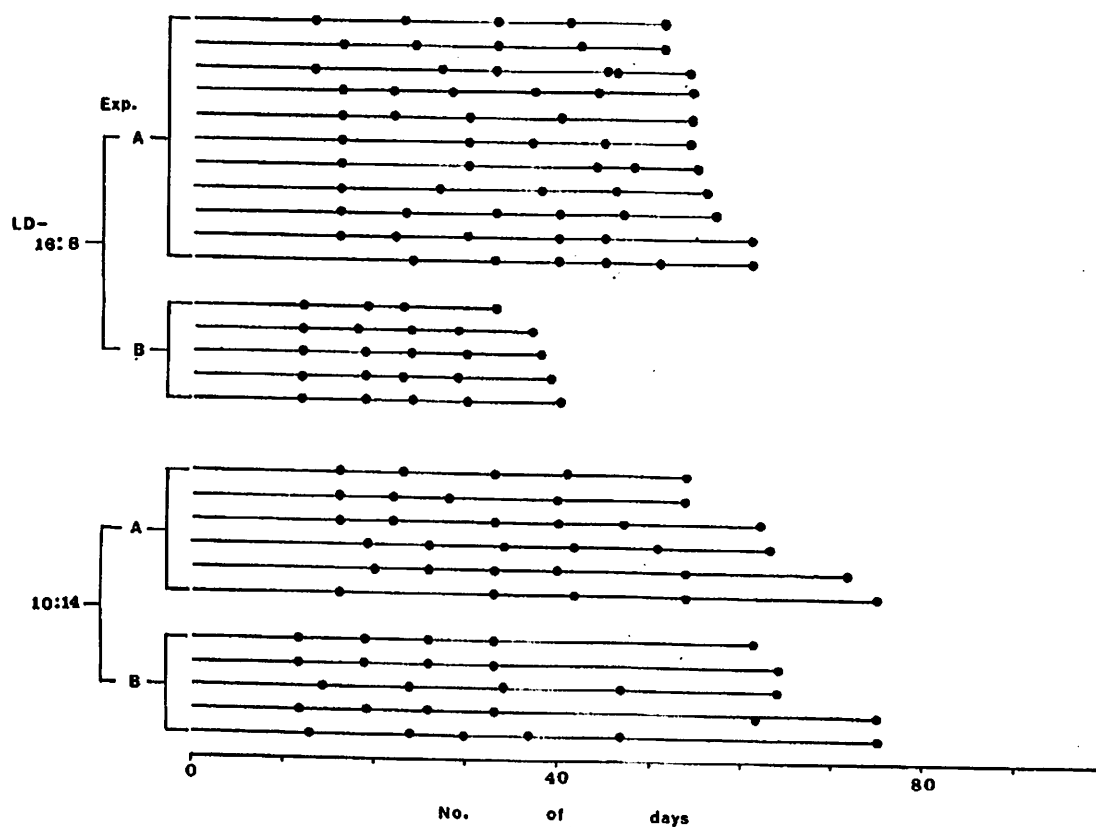


Fig. 1.—Development of males reared at 25°C and 16L-8D or 10L-14D. The length of horizontal line indicates the number of days required for development in each individual. Solid circle shows molt. In experiment A feeding intervals were 3-4 days, in experiment B 2-3 days for first and second instars.

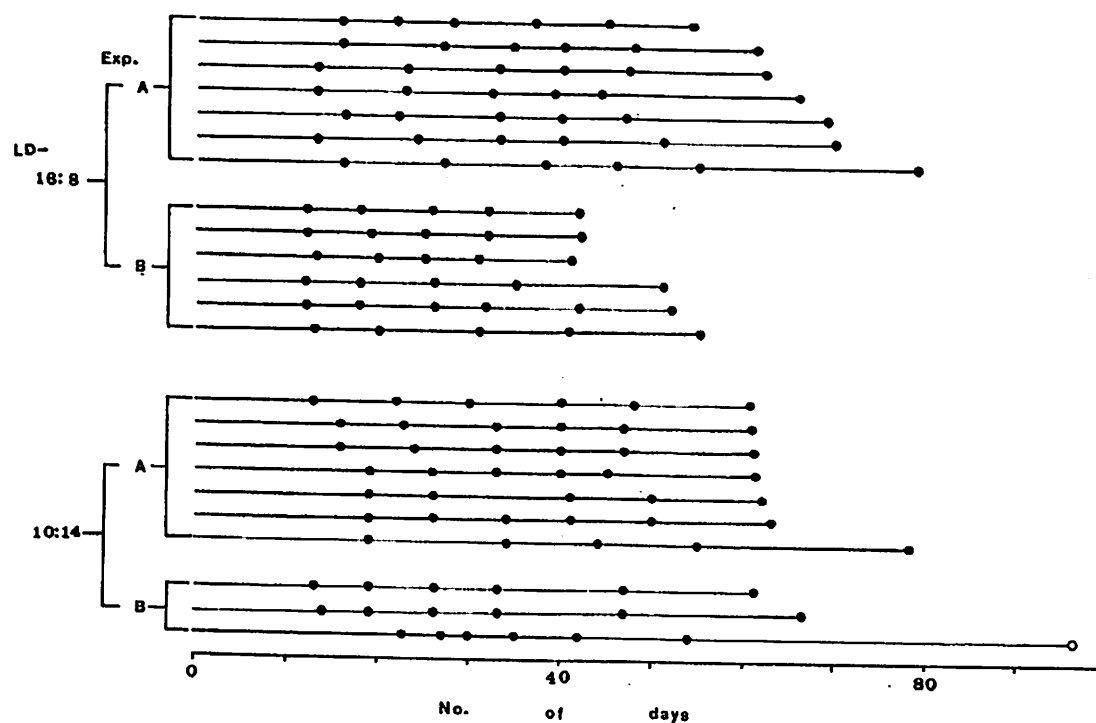


Fig. 2.—Development of females reared at 23°C and 16L-8D or 10L-14D. Symbols and experimental conditions are the same as in Figure 1. The bottom horizontal line with a hollow circle on the tail indicates the individual that passed the longest last instar and molted seven times.

Table 1—Carapace widths of adult *A. tepidariorum* obtained from laboratory rearings vs those collected from the field. The former were the individuals obtained from the experiments shown in Figs. 1, 2, and 3, and the latter those used for the experiment in Fig. 4.

Source	Sex	No. of molts	No. of indiv.	Mean (mm)	Range (mm)
Laboratory	Males	4	1	1.31 —	—
		5	20	1.50 ± 0.14†	1.31 — 1.75
		6	6	1.52 ± 0.08	1.38 — 1.63
		Total	27	1.49 ± 0.21	1.31 — 1.75
Laboratory	Females	5	3	1.71 ± 0.03	1.69 — 1.75
		6	12	1.83 ± 0.13	1.63 — 2.06
		7	1	2.25 —	—
		Total	16	1.95 ± 0.22	1.63 — 2.25
Field	Females	Unknown	16	2.16 ± 0.19*	1.94 — 2.41

† SD, \* Significant in *t*-test(5%).

It should be noted that the body size of the females reared in the laboratory was significantly smaller than that of the individuals collected from the field (Table 1). Schaefer (1977) also noted that the body size of the reared *Clubiona phragmitis* C. L. Koch was smaller than that of individuals collected from the field. The cause(s) are unknown, but it could be due to a simplified menu in the laboratory rearing.

**Development under complete darkness.**—Fig. 3 shows the development under complete darkness as compared with that under 14L-10D. The graph shows that development under complete darkness proceeded more speedily than under 14L-10D. In four of the five females, the number of molts was also reduced. It can be said from these results that this spider is able to perform prey capture and feeding normally without visual sense. However, the reason why the development is accelerated under complete darkness is not understood.

**Effects of photoperiod on egg sac production.**—Fig. 4 shows the egg sac production of 15 females reared under either long or short photoperiod. The females which mated successfully either in the field or in the laboratory produced egg sacs during 2/3 or more of life span, irrespective of the difference in photoperiod. When mating was delayed, egg sac production was also delayed. When mating was prohibited, no egg sac was produced, except for one female which produced a sterile egg sac. It seems that the female receives enough spermatozoa to fertilize almost all the oocytes in her body by a single mating.

The number of egg sacs produced per female differed from individual to individual. In addition, sterile egg sacs were occasionally produced in a series of otherwise healthy egg sacs. The total healthy egg sacs per female varied from 5 to 15. The mean was  $9.7 \pm 2.9$  when three females which were prohibited to mate were excepted. Similarly, the mean egg sac production interval was 8.1 days when the sterile egg sacs were included. The mean egg sac production intervals for each individual are shown by the figures attached on the tails of each horizontal line in Fig. 4. The mean longevity was  $116.5 \pm 10.3$  days. The mean egg period from egg sac production to the emergence of spiderlings was  $11.0 \pm 1.5$  days.

In males reared under the same conditions, the mean longevity was  $33.9 \pm 4.4$  days.

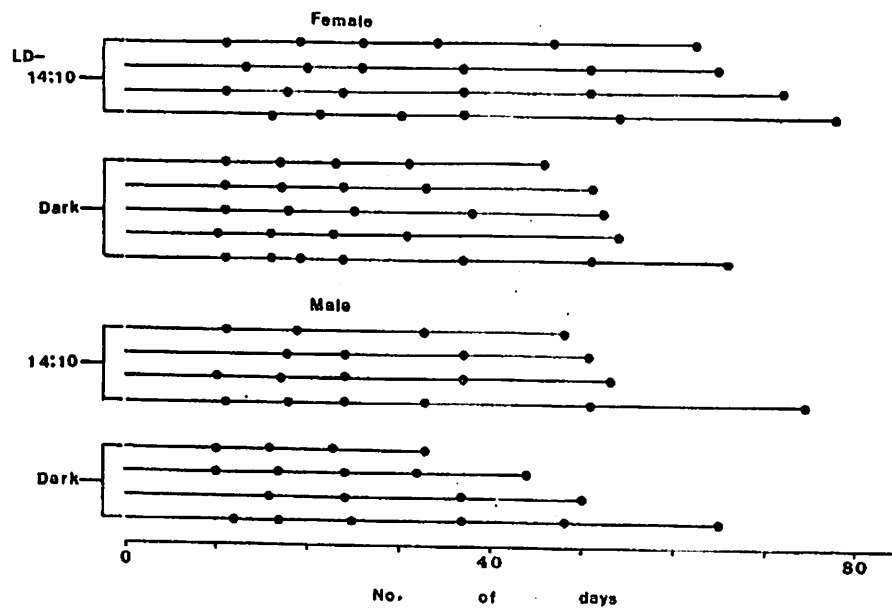


Fig. 3.—Development in both sexes reared at 23°C in complete darkness or 14L-10D. Symbols are the same as in Figure 1. Feeding intervals were 3-4 days.

**Egg number per sac in relation to egg sac sequence.**—Fig. 5 shows the relationship between the number of eggs per sac and egg sac sequence. In the graph, the sterile eggs were included in counts of the egg sac sequence but omitted in the calculation of the egg number per sac.

As shown by vertical lines, the range of variation in the egg number per sac was large irrespective of the egg sac sequence. However, the mean number of eggs per sac shows a gradual decrease with time. This tendency somewhat differs from that reported by Valerio (1976). He investigated egg sac productions at natural

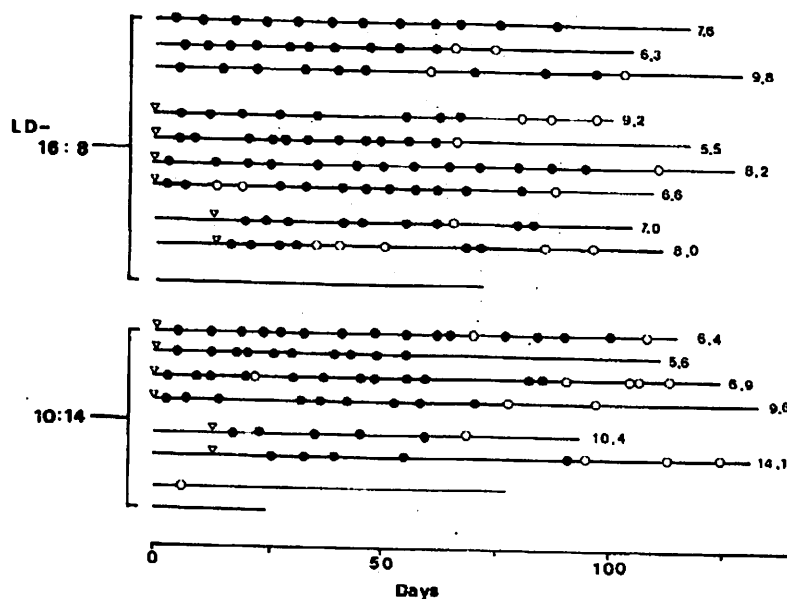


Fig. 4—Egg sac production at 25°C and 16L-8D or 10L-14D. Feeding intervals were 3-4 days. The lengths of horizontal lines indicate longevities in days for each female. Solid or hollow circles show healthy or sterile egg sacs, respectively. The upper three individuals were females mated in the field, and triangles indicate matings in the laboratory. Figures attached on the tails of each line indicate the mean interval between egg sacs.

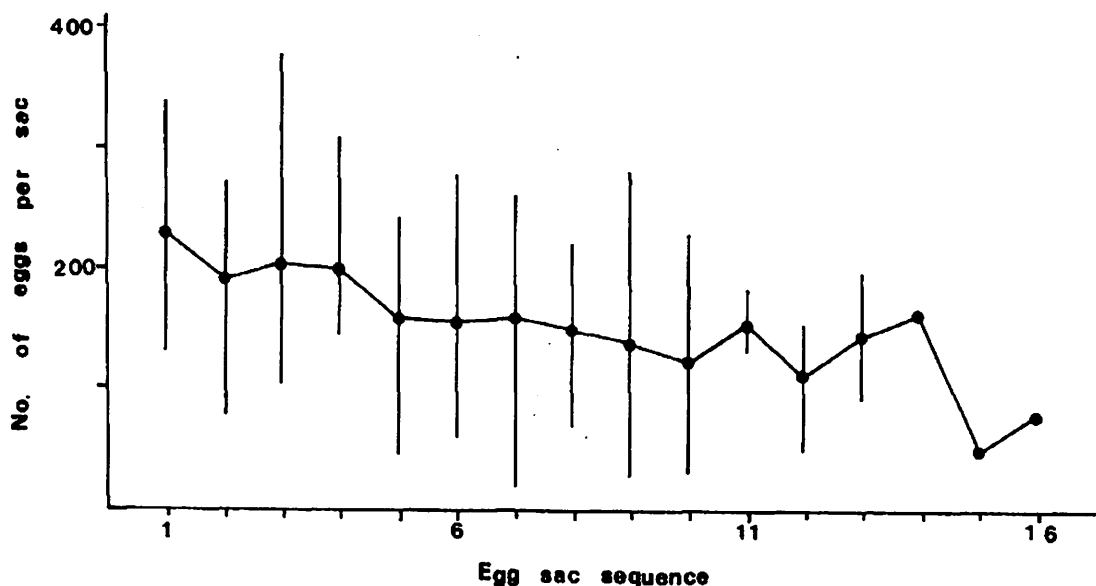


Fig. 5—The relationship between egg number per sac and egg sac sequence. Vertical lines and solid circles indicate the ranges and means of egg number per sac in relation to position in the sequence.

room temperature in the tropics, Costa Rica, and presented the result which indicated a downward curve with two peaks related to the females' ages.

The mean total egg number produced per female was 1812.7. This figure was quite small as compared with Valerio's 3211.9 in the tropics. As shown in Fig. 4, the female continued to produce egg sacs through 2/3 of her life, but the frequency of sterile egg sacs was somewhat increased in the latter half of adult life. In addition, several females began to construct incomplete, thin egg sacs from which eggs often dropped out when touched.

## DISCUSSION

The development of the house spider seems to be very flexible. As shown in Figs. 1 and 2, when food conditions were favorable, the development at 25°C and long photoperiod was accelerated by omission of one or two molts. According to Kaston (1970), even under careful rearing at 25°C, the number of molts varied from three to six in the male and five to eight in the female of *Latrodectus hesperus* Chamb. and Ivie, and three to seven in the male and five to eight in the female of *L. mactans* Fabr. The same fact was also reported by Schaefer (1977) in *Clubiona phragmitis* C. L. Koch, *Tetragnatha montana* Simon, and *Alopecosa accentuata* (Latreille), and by Mansour et al. (1980) in *Chiracanthium mildei* L. Koch. Deevey (1949) reported that the developmental period and the number of molts in *L. mactans* were strongly affected by the available food amount. Miyashita (1968) also reported the same fact in *Lycosa t-insignita* Boes. and Str. It can be said, therefore, that the developmental flexibility of the house spider is connected closely to such a variability in number of molts. In addition, this flexibility will be reinforced further by a strong resistance to fasting. As shown in Table 2, the spiderlings emerging from the egg sac could survive for 16-30 days without food and water. It is of interest that the mean longevity was significantly shorter when they were kept in solitary than when kept in a group. The reason for this is unknown.

Table 2.—Mean longevities in days of spiderlings in solitary and group under fasting at 23°C and 4L-10D.

Condition	No. of indiv.	Longevity	
		Mean	Range
Solitary	33	15.5 ± 1.5†	12-23
Group	38	30.4 ± 1.8**	14-36

† SD, \*\* Significant in *t*-test (1%).

According to Schaefer (1977), there are two different groups among spiders in reaction to photoperiods, one retains normal development irrespective of the difference in photoperiod, and the other retards development under short photoperiod. If we follow this classification, the house spider seems to belong to the latter group. Hamamura (1982) reported that in *Philodromus subaureolus* Boes. and Str., the development in early life was accelerated by a short photoperiod but retarded by a long one, although this characteristic was reversed in overwintered nymphs developed up to middle stage.

In the house spider, a developmental acceleration occurred under the long photoperiod when food conditions were favorable, but a prolongation of the last instar or both the last and penultimate instars occurred under the short photoperiod (Fig. 1). This characteristic seems to have a close connection with the overwintering of this species. In the field, overwintering populations generally consisted of nymphs at different instars and of adults, but mainly nymphs, in the last instar or the penultimate one. Such a structure of the overwintering population will reasonably be explained by the above-mentioned characteristics in reaction to the short photoperiod, since egg sac production in the field mainly occurs during June and July.

When the overwintering nymphs were collected from the field at different dates during winter and early spring, and incubated at 23°C and 14L-10D, the length of period from the commencement of incubation to the resumption of molting became gradually shorter from winter to early spring as shown in Table 3. The same phenomenon was already reported by Miyashita (1969) in *L. t-insignita*, but in the house spider, the shortening degree in that length was rather small. Among overwintering adult females, both mated and virgin individuals were included, and the former collected in December of the previous year and January began to

Table 3.—Change in the period from the commencement of incubation to molt occurrence in the overwintering nymphs collected on four different dates. Incubation was made at 23°C and 14L-10D.

Condition	No. of indiv.	Longevity	
		Mean	Range
25 Dec. 1983	Female	4	
	Male	1	15.2 ± 3.5†
15 Jan. 1984	Female	3	10-21
	Male	2	14.4 ± 2.8†
16 Feb. 1984	Female	4	11-20
	Male	2	11.2 ± 1.3†
24 Mar. 1984	Female	2	3-13
	Male	3	8.0 ± 0.9†

† SD

produce egg sacs after 20-30 days from the commencement of incubation. When the females which had developed to the adult stage during incubation were mated with the males obtained under the same condition, they began to produce egg sacs only 10 days from that mating. In addition, as shown in Fig. 4, egg sac production in the female was scarcely affected by photoperiod. It appears that the overwintering individuals are in a status similar to dormancy or diapause among certain insects and mites, but the degree of the spider's dormancy is not so strong, because every individual resumes feeding soon after the commencement of incubation. Bonnet (1935) inferred that this spider originated in the tropics. If this is true, an acquisition of the above-mentioned characteristics will probably have had an adaptive significance for expanding their habitat into the temperate regions of the world.

### ACKNOWLEDGEMENTS

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**EGG PRODUCTION OF *ACHAEARANEA*  
*TEPIDARIORUM* (C.L. KOCH)  
(ARANEAE, THERIDIIDAE) IN THE FIELD IN JAPAN**

This field survey on the egg production of *Achaeearanea tepidariorum* (C. L. Koch) in Japan was made in 1984 to compare with the results of a laboratory investigation which was reported separately (Miyashita, K. 1987. J. Arachnol. 15:51-58).

The survey was conducted in a vacant house in Abiko City (140°02'E, 35°52'N), Chiba Prefecture. Adult females, which spun webs on the wall, at the edges of the verandah, and under the floor, were carefully observed and censused daily from May to September. When new females were found, they were recorded and marked with colored paint, and the dates of egg sac productions and disappearances of females themselves were recorded. Egg sacs were removed from webs on the 7th or 8th day after oviposition and kept separately in glass vials. The number of spiderlings that emerged was considered as an indicator of the number of eggs in the sac, since healthy egg sacs rarely contained non-viable eggs.

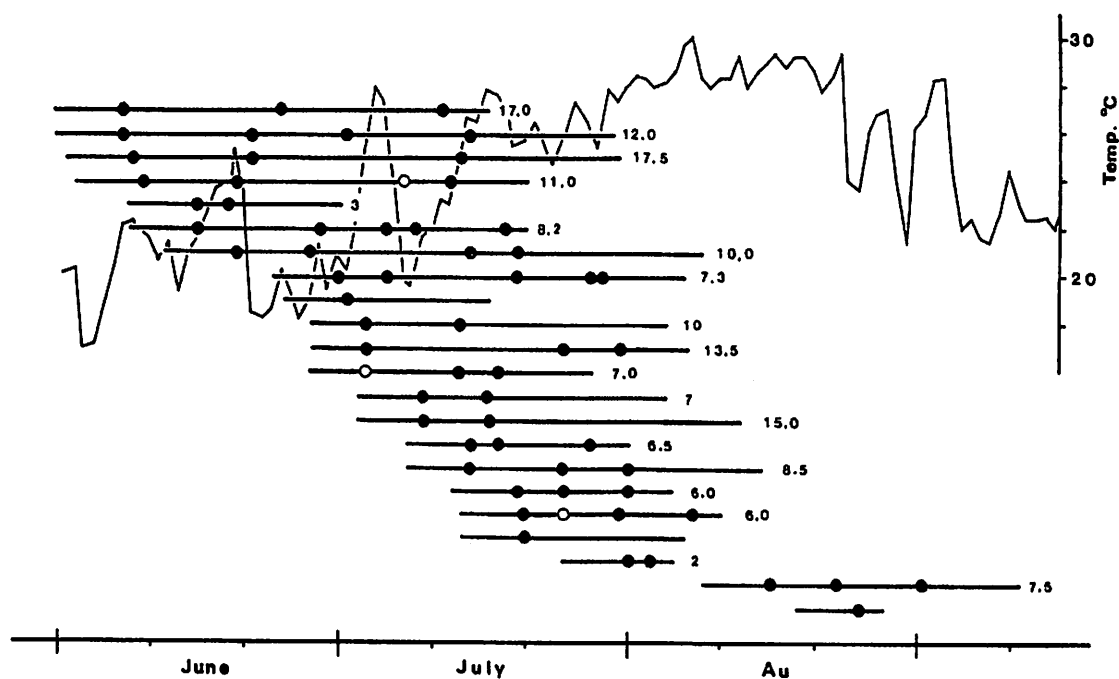


Fig. 1.—Seasonal changes in the resident periods and egg sac production of 22 females *Achaeearanea tepidariorum* in the field. Horizontal lines indicate length of resident periods in days. Solid or hollow circles show healthy or sterile egg sacs, respectively. The figures following each line are the mean interval(days) between egg sacs. The fine line shows the change of daily mean temperatures.

Figure 1 shows the seasonal changes in length of the resident periods of females and the intervals between egg sacs. "Resident period" means the period from the date of first appearance to that of disappearance of each female. The cause(s) of disappearances were not ascertained. The rate of appearance of adult females increased gradually from early June to late July, and decreased sharply thereafter.

The total number of adult female residents was 22, some were residents as juveniles and others were invaders from outside. The resident period became shorter for individuals that appeared late in the season (mean =  $35.1 \pm 14.0$  days).

Egg sac production began in early June, reached a peak in the middle of July, and ceased by early September. Observations outside the survey site, however, showed sporadic egg sac production from the middle of May to late October, although that production was rare. It appears that temperature changes had no apparent effect upon the egg sac production (Fig. 1).

The number of egg sacs per female varied from 1 to 5, (mean = 2.9) including sterile egg sacs produced by three females. The mean interval between egg sacs was  $9.4 \pm 5.6$  days. The number of eggs per sac varied from 150 to 650, (mean = 310.8) excluding sterile egg sacs. In 14 among the 64 egg sacs examined in total,

Table 1.—“Egg periods” in days examined in June, July and August.

Season	No. of egg sacs	Mean	Range
Early June	4	15.4	14-18
Early July	7	11.3	8-15
Early Aug.	6	10.4	8-13

females produced egg sacs a few days after they had captured a large prey. The interval between egg sacs and the number of eggs per sac seemed to be influenced by the nutritional condition of the female. The number of total eggs produced per female varied from 242 to 1866 (mean = 881.7).

In the laboratory, each of 15 females produced 9.7 egg sacs containing a total of 1812.7 eggs at intervals of 8.1 days in average (Miyashita, K. 1987. *J. Arachnol.* 15:51-58).

Valerio (1976. *Bull. British Arachnol. Soc.*, 3:194-198) examined egg sac production in tropical Costa Rica and reported that, although one female produced 20 sacs, the mean number of sacs per female was 14.1, and that the mean number of eggs per female was 3211.9. Valerio's search of the literature showed that the number of egg sacs produced per female in the temperate regions ranged from 4 to 7 except for one record of 17 reported by Bonnet (1935. *Bull. Soc. Hist. Nat. Toulouse*, 68:335-386).

As shown in Table 1, the “egg period”, which means the number of days from egg sac production to the spiderlings' emergence, became shorter later in the season. This may be influenced by rising temperatures at that time. In the laboratory at 25°C, the mean egg period was 11.0 days.

Kazuyoshi Miyashita, Department of Biology, Faculty of Science, Tokyo Metropolitan University, Setagaya-ku, Fuakazawa 2-1-1, Tokyo 158, Japan.

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## Seasonal Life Cycle of the House Spider, *Achaearanea tepidariorum* (Araneae: Theridiidae) in Northern Japan<sup>1</sup>

Kazuhiro TANAKA<sup>2</sup>

*Laboratory of Entomology, Faculty of Agriculture,  
Hirosaki University, Hirosaki 036, Japan*

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The seasonal life cycle of the house spider, *Achaearanea tepidariorum*, was investigated in the field at Hirosaki, Aomori prefecture. Spiders of all nymphal instars and adults were found throughout the year and the overwintering stage was not restricted to a particular developmental stage. The reproductive activity occurred for a long period of time from June to October. The seasonal occurrence of adult males, the egg laying pattern and its geographical variation suggested that in spite of such life cycle characteristics, this species is basically univoltine throughout Japan. The variability of its overwintering stage may have evolved in association with the scattered emergence of the spiderlings over a long period of time.

### INTRODUCTION

The house spider, *Achaearanea tepidariorum*, is a common species and its occurrence is frequently associated with human dwellings. This species was first described from a green house in Germany (LEVI, 1967), but it is widely distributed in various parts of the world (YAGINUMA, 1986). Since many of its relatives occur in South America, LEVI (1967) inferred that this spider probably originated there and was introduced with plants by man to various parts of the world.

In Japan, it is often found on outside walls of buildings, but our knowledge of its life history or other aspects of its ecology is scanty. ORI (1975) made monthly collections of egg-sacs and recorded the seasonal fluctuation of the population density and prey items and showed that the peak of the population density at Nagasaki occurred in June or July and most egg-sacs were produced in May to August.

In order to elucidate the seasonal adaptation of the house spider, I studied its seasonal life cycle at Hirosaki, Aomori prefecture. In this report, I describe the results of field survey and discuss some aspects of the life cycle characteristics.

### MATERIALS AND METHODS

I collected spiders monthly from January to December, 1984, and from July to October, 1986, on the campus of Hirosaki University. As an indicator of body size, the carapace width of the collected spiders was measured using an ocular micrometer

<sup>1</sup> Contribution No. 106 from the Laboratory of Entomology, Faculty of Agriculture, Hirosaki University.

<sup>2</sup> Present address: *Laboratory of Applied Zoology, Faculty of Agriculture, Hokkaido University, Sapporo 060, Japan*

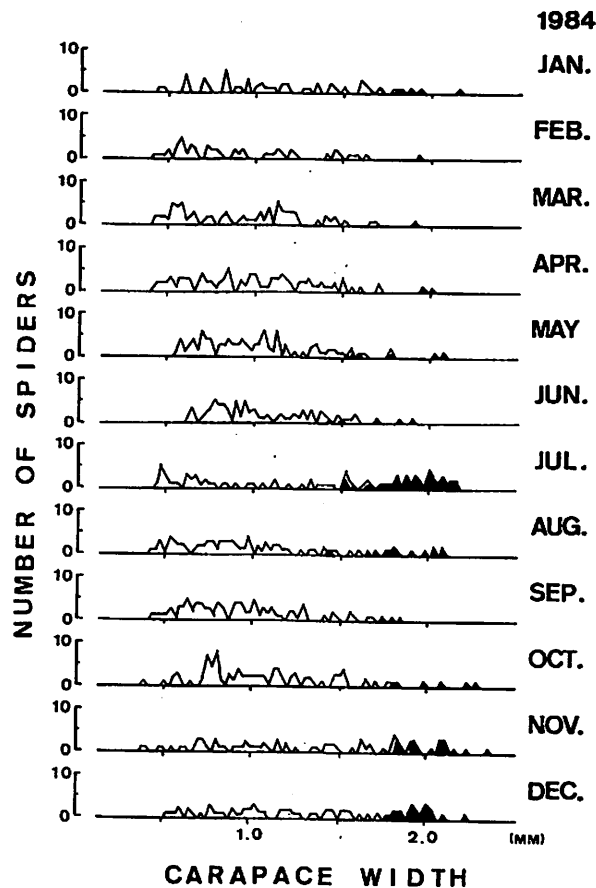


Fig. 1. Carapace width distribution in monthly samples of *Achaearanea tepidariorum* collected at Hirosaki in 1984. Closed portions represent adults.

( $1=1/40$  mm). After the measurement, they were returned to the collecting spots.

To determine the overwintering stage, spiders just after hibernation were collected at several sites in Hirosaki City in March, 1985 and 1986, and the carapace width was measured.

Adult males were counted weekly at two sites on the campus: the southern wall of a building (site A) and the eastern side of a block fence facing a street (site B). The counts were made from 1985 to 1987 at site A and in 1987 at site B. As an indicator of the seasonal abundance, I counted spiders spinning web on the wall below window frames of the ground floor at site A in 1985 and 1986. Also I counted the newly produced egg sacs weekly in 1985 to 1987 and marked each female that had produced an egg sac by fixing a numbered piece of sticky tape on the wall at site A to elucidate the reproductive history of each female. Daily temperature on the campus from 1985 to 1987 was obtained from the meteorological records of Hirosaki University.

## RESULTS

### *Seasonal change in body size*

The frequency distributions of carapace width in monthly collections are shown in Figs. 1 and 2. Although the instar of this spider can not be determined exactly by

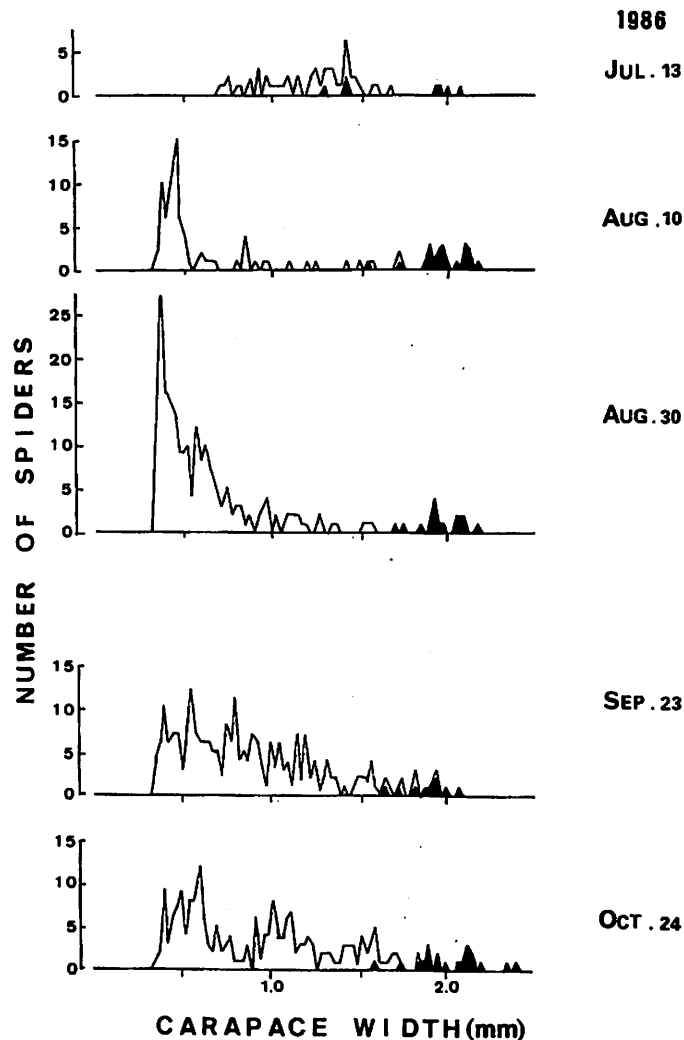


Fig. 2. Carapace width distribution in samples of *Achaearanea tepidariorum* collected at Hirosaki from June to October in 1986. Closed portions represent adults.

the size of carapace width, the frequency distribution may represent the seasonal succession of the instars. In 1984, spiders of all nymphal instars and adults were found throughout the year (Fig. 1). This may be one of the characteristics of the life cycle of this species. Although the development is not highly synchronized, the proportion of adults in the monthly samples rapidly increased in July (Table 1).

Figure 3 shows the seasonal occurrence of adult male. The seasonal occurrence of male adults in site A varied from year to year. In 1985, many males were found in autumn, but in 1986 and 1987, the number of adult males rapidly decreased in autumn.

Spiderlings of which the carapace width are less than 0.5 mm were not observed in May and June, 1984, but they began to appear in July (Fig. 1). Similarly, no spiderlings were found in July, 1986, but the emergence began to occur in August (Fig. 2). There seemed to be a mechanism regulating the seasonal development or reproduction despite that overwintering in this species is not limited to a particular developmental stage. This was also suggested by samples obtained just after hibernation in March, 1985 and 1986 (Fig. 4). Namely, the spiders hibernated at any

Table 1. Seasonal change of proportion of adult spiders in the monthly collection, 1984

Month	No. of samples	Adult (%)
Jan.	52	11.5
Feb.	50	2.0
Mar.	79	1.3
Apr.	93	2.2
May	100	6.0
Jun.	77	6.5
Jul.	83	44.6
Aug.	82	17.1
Sep.	95	3.2
Oct.	89	7.9
Nov.	77	27.3
Dec.	69	29.0

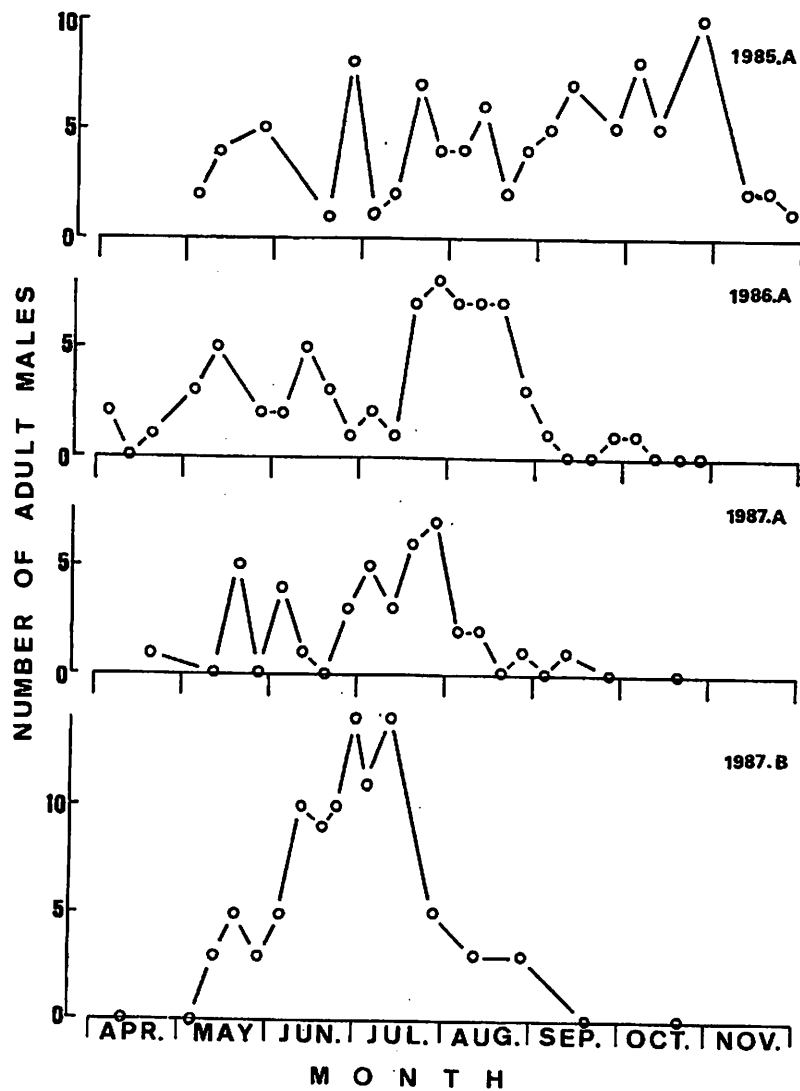


Fig. 3. Seasonal occurrence of adult males at Hirosaki.

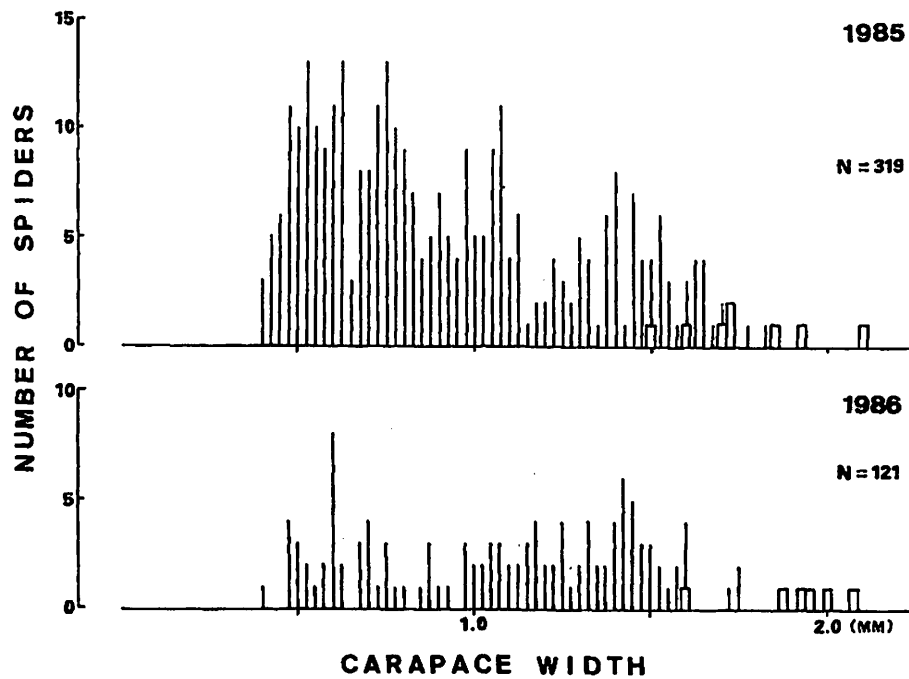


Fig. 4. Carapace width distribution in overwintering samples of *Achaearanea tepidariorum* at Hirosaki. Bars represent nymphs and histograms adults.

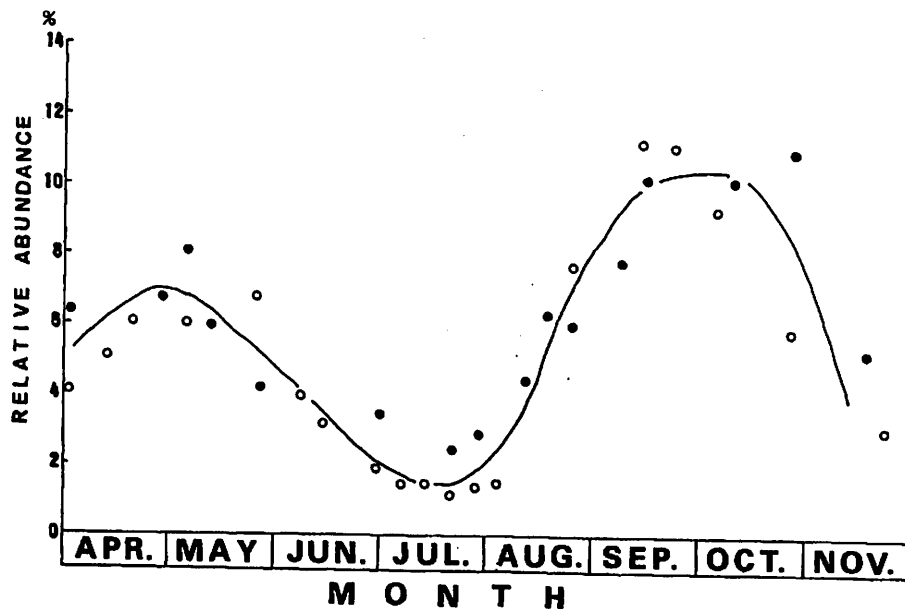


Fig. 5. Seasonal fluctuation in abundance of *Achaearanea tepidariorum* at Hirosaki in 1985 (closed circles) and 1986 (open circles). The abundance of spiders is expressed as percentage of the total 2,737 in 1985 and 3,434 in 1986 throughout the season.

nymphal or the adult stage, but the proportion of adults in the overwintering population was low (2.5% in 1985 and 5.0% in 1986) and hibernating eggs were not found.

#### *Seasonal change in population density*

The seasonal change in abundance of this spider was investigated by counting

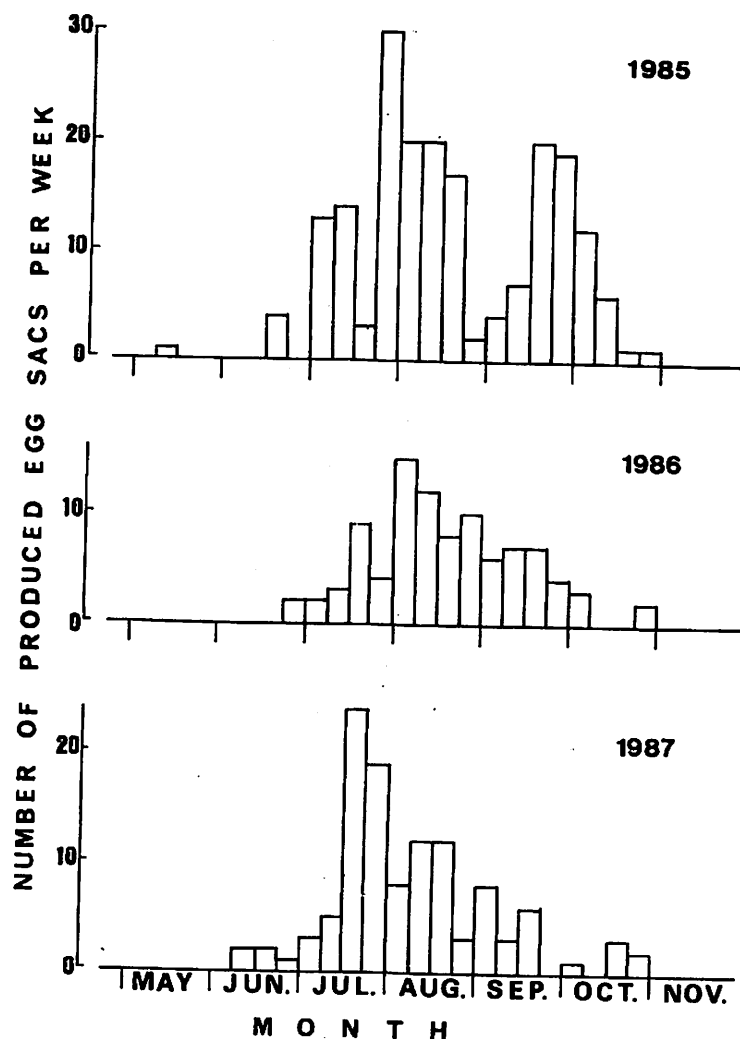


Fig. 6. Seasonal distribution of egg-sac production in *Achaearanea tepidariorum* at Hirosaki.

active spiders (occupying a web). The results are shown in Fig. 5. Each count is expressed as percentage of the seasonal total.

The number of active spiders after hibernation gradually decreased in May and reached a minimum in July. Then, it increased rapidly in August and a peak was reached in September. The increase in summer might be due to newly hatched spiderlings. The pattern of seasonal fluctuation in abundance was similar in 1985 and 1986.

#### *Reproductive season*

The season of reproduction, together with the overwintering stage, characterizes the life cycle pattern. The reproductive activity is represented by the seasonal occurrence of the newly produced egg sacs.

The egg sacs were produced from mid-May to late October in 1985, from late June to late October in 1986 and from mid June to late October in 1987 (Fig. 6). Thus, this spider has a relatively long reproductive period. However, the seasonal occurrence of egg sacs somewhat varied from year to year. In 1985, many egg sacs were produced in late July and the number rapidly decreased in late August and increased



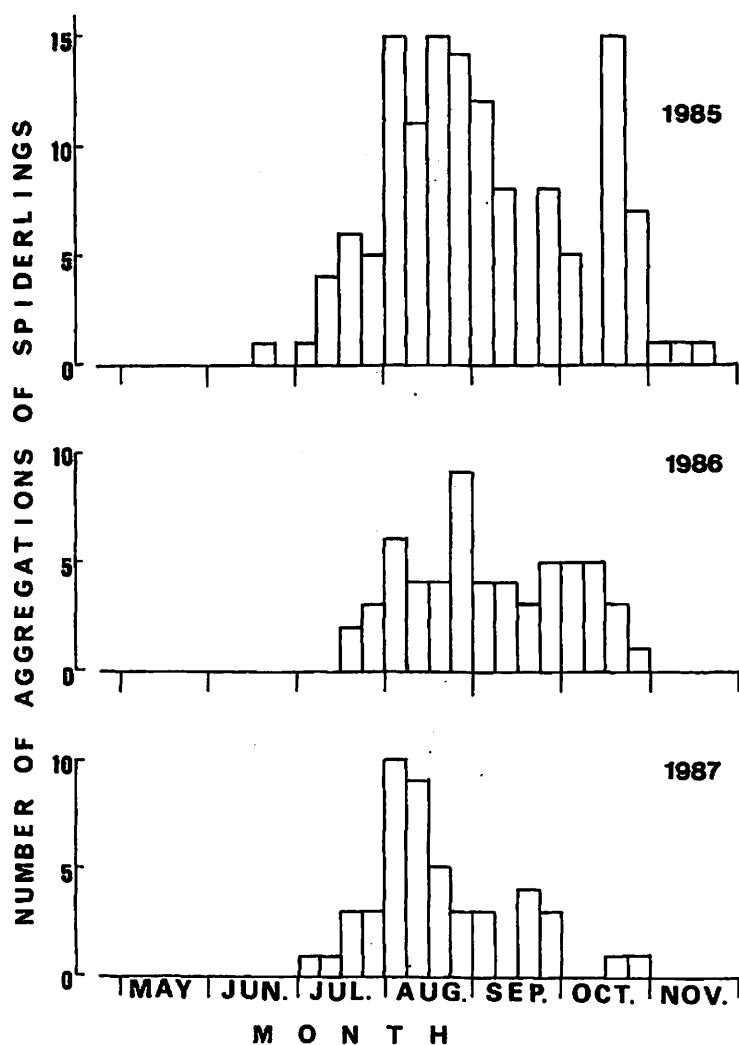


Fig. 7. Seasonal occurrence of spiderling aggregations of *Achaearanea tepidariorum* at Hirosaki.

again in September. Thus, the seasonal egg-sac production in 1985 was bimodal with peaks in summer and early autumn, respectively. On the other hand, in 1986 and 1987, the oviposition was of a unimodal pattern with a peak in summer and egg sacs decreased in autumn.

Females produced  $2.3 \pm 1.1$  and  $2.8 \pm 1.7$  ( $\pm$ s.d.) egg sacs during the two or three month period in 1986 and 1987, respectively. In one of the extreme cases, a female produced seven egg sacs in 3 months.

Since spiderlings aggregate by the egg sac immediately after emergence and stay there for a day, we can infer the time of their emergence from such aggregations. The emergence from egg sacs began in mid June, 1985, mid July, 1986, and early July, 1987, about one month earlier in 1985 than in 1986 (Fig. 7).

#### DISCUSSION

At Hirosaki ( $40^{\circ} 30'N$ ), oviposition of *Achaearanea tepidariorum* usually occurs for a

long period from June to October (Fig. 6). Egg sac counts showed a bimodal curve in 1985, but unimodal ones in 1986 and 1987. The seasonal occurrence of adult males showed a more or less corresponding fluctuation (Fig. 3). In 1985, therefore, many adult males and egg sacs were observed from September to October. Such abundance of adult males and egg sacs in autumn may suggest a partial occurrence of bivoltine cycle in 1985. The mean summer temperature from July to August in 1985 was about 2.7°C higher than that in the other years. This may support the inference of the partial bivoltine cycle in 1985.

The egg laying period may vary geographically. For example, in Naha, Okinawa (26°14'N), many females have produced several egg sacs already in April (YAMAGISHI, personal communication). In Nagasaki (32°44'N), egg sacs are produced from March to October, most of them from May to July forming a peak in June (ORI, 1975). Moreover, in Abiko, Chiba (35°52'), egg sacs are produced from mid-May to late October, most of them from early June to August with a peak in mid-July (MIYASHITA, 1987). Thus, the egg sac production begins earlier in the southern localities. Nevertheless, the egg laying pattern in Nagasaki is unimodal, suggesting a univoltine life cycle. It is noticeable that, in Nagasaki, the number of egg sacs rapidly decreases after the peak and reaches a very low level in August when the temperature is high. A similar tendency in egg laying pattern is observed in Chiba by MIYASHITA (1987). It seems, therefore, that this spider is basically univoltine throughout Japan. This contradicts with the inference of a partial bivoltine cycle in Hirosaki in 1985. If the life cycle can vary between univoltine and bivoltine with the climatic conditions, a bivoltine life cycle will be predominant in southern localities. However the predominant life cycle there is univoltine (ORI, 1975). This may suggest that the seasonal distribution of egg sacs may not be an indicator of voltinism. In an iteroparous species with a relatively long life span, the reproductive activity may be overlapped among different generations. Therefore, the egg laying pattern is not always appropriate for the indicator of generation number. Because of this, we have to use several life cycle characteristics to determine the voltinism. The univoltine life cycle of this spider is suggested by the seasonal abundance. At Nagasaki, the seasonal population trend showed a unimodal pattern with a peak in June or July (ORI, 1975). At Hirosaki, it was also unimodal, but the peak was reached in September or October (Fig. 5). This difference in peak time may be due to the local difference in the beginning of the reproductive season. This comparison makes it uncertain that a bivoltine life cycle occurs in Hirosaki. The life cycle in Hirosaki seems to be univoltine. However some spiders that had once hibernated remained at the earlier nymphal instars even in July, 1984 and August, 1986 when newly hatched spiderlings began to emerge (Figs. 1 and 2). Probably these spiders can not complete their nymphal development within a summer and may hibernate the second winter at the later nymphal stage. The life cycle in Okinawa is not well known.

Samples taken from the overwintering population in 1985 and 1986 included all nymphal instars and adults (Fig. 4). This indicates that the overwintering stage of this spider is not restricted to a particular developmental stage. Such flexibility of overwintering is one of the characteristics in the life cycle of this spider.

Similar flexibility in the overwintering stage was found in several insect species. The collembolan, *Lepidocyrtus lignolum*, can hibernate at all developmental stages from egg to adult (LEINAAS and BLEKEN, 1983). However, in most cases, the variability is

found as different overwintering instars of the larval stage. In the two species of ant-lion, *Myrmeleon formicarius* and *Hagenomiya micans*, overwintering is restricted only to the larval stage, but any of the three larval instars can hibernate (FURUNISHI and MASAKI, 1982). In these pit-fall hunters, it is inferred that the variability of overwintering instar may have evolved as a means to tolerate unpredictable and intermittent food supply. Some species of insects show geographical variation in the overwintering stage. In the pine moth, *Dendrolimus spectabilis*, the geographical variation of the overwintering stage is closely related to the local life-cycle variation (HABU, 1976).

In the house spider, the ecological significance of the variable overwintering stage seems to be different from the above examples. The long oviposition period of this spider (Fig. 6) results in widely scattered hatching of spiderlings (Fig. 7). Because of this, their growth status in relation to the seasonal change is highly variable. If overwintering is restricted to a certain developmental stage, late-hatching spiders would fail to reach, or early-hatching ones would pass through, that stage before winter and suffer high winter mortality. The ability to hibernate at any developmental stage may increase their winter survival. Thus, the flexibility of the overwintering stage in this species may have evolved in association with the long and scattered emergence of spiderlings.

The seasonal life cycle of this spider is thus characterized by relatively long reproductive period and the flexibility of overwintering stage. These characteristics would result in scattered emergence of adults. Nevertheless, the occurrence and activity of reproductive adults in the field are seasonally controlled. This will be the subject of my next paper.

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## **THE SIZE OF SPIDER EGGS AND ESTIMATES OF THEIR ENERGY CONTENT**

**John F. Anderson**

Department of Zoology  
University of Florida  
Gainesville, Florida 32611 USA

### **ABSTRACT**

Egg size was used to estimate the energy incorporated into egg production in a sample of 24 species representing 11 families. Egg mass scaled geometrically to egg diameter. Egg mass can be accurately estimated from the easily measured diameter of an egg. Comparison of egg sizes between populations of seven species common to Connecticut and Florida suggest egg size is species-specific. The constancy of energy density of spider eggs allows relatively accurate estimates of the energy incorporated into egg production using easily obtained data on egg size, number of eggs per clutch, and number of clutches.

### **INTRODUCTION**

A basic consideration in most studies of spider reproduction relates egg production to energy availability (Craig 1987). In general, the number of clutches and number of eggs per clutch is determined by food supply (Bristowe 1958; Riechert and Tracy 1975; Enders 1976; Eberhard 1979; Craig 1987).

Studies emphasizing energetic costs of producing eggs exhibit a potential problem, namely the difficulty of measuring all the components necessary to estimate such costs. Single indices such as egg number (Petersen 1950; Enders 1976; Valerio 1976; Miyashita 1987a,b; Roach 1988; DeKeer and Maelfait 1988) and egg mass (Taylor and Peck 1975; Riechert and Tracy 1975; Killebrew and Ford 1985; Morse 1987) have been used as estimates of the energy incorporated into egg production. Use of single indices requires certain assumptions to make valid comparisons. For example, comparison of egg number assumes egg sizes are equal among the compared groups. A complete estimate of such costs over the life span of a female spider requires data on the number of clutches, the number of eggs per clutch, egg size, and energy density of the eggs. The fact that these studies are incomplete in this context is evidence of the very real difficulties of obtaining such data.

A major problem in this context is measurement of energy density. Accurate estimates using bomb calorimetry are time consuming and require skill, dedication, and careful attention to numerous procedural details (Phillipson 1964; Paine 1971; Anderson 1978). The time and labor involved justifies search of other methods of estimating relative energy content of eggs. Analysis of inter- and intraspecific variation of clutch size, egg size, and energy density indicate the

latter is the least variable (Anderson 1978). Killebrew and Ford (1985) argued that mass per newly hatched spiderling, and by extension, egg mass, in any one species is "optimized by natural selection." If correct, egg size might provide a practical and reasonably accurate measure of the energy content of a spider egg.

Here I evaluate egg size, measured as a linear dimension, to estimate egg mass. Linear dimensions of eggs can be easily and accurately measured using dissecting microscopes common to most laboratories. My specific aims were to determine whether egg size is species-specific and, if so, to describe the relationship between diameter and egg mass.

## METHODS AND MATERIALS

Egg sacs of various species were collected from habitats around Gainesville, Florida. Although I picked species based on availability of reproductively active females, some effort was made to choose those which provide a reasonable range in the measured parameters. Of the 24 species considered here, data for 12 were obtained from a previous study (Anderson 1978).

Eggs were removed from egg sacs and counted. Their total wet mass was immediately measured to the nearest 0.1 mg and the average mass per egg determined by calculation. Egg diameter was measured to the nearest 0.01 mm with a dissecting microscope fitted with a calibrated ocular on a minimum of ten eggs per egg sac. Since few eggs are exactly spherical, the reported diameters represent the average of measurements made on the longest and the shortest axis of an egg. Differences between these two measurements of all samples averaged 7%.

Assuming geometric similarity obtains, i.e., shape and density are constant, the mass of an egg would be proportional to diameter<sup>3</sup> where the latter represents a characteristic linear dimension (McMahon and Bonner 1983). Consequently I fitted the data to the power function  $EM = aED^b$ . Here  $EM$  represents egg wet mass;  $ED$  is egg diameter;  $a$  is a proportionality constant and  $b$  is the exponent of the function. The parameters  $a$  and  $b$  were calculated by least squares analysis of paired data after transformation to common logarithms. Correction for bias in log-transformed data (Sprugel 1983) made in estimating the proportionality constant ( $a$ ) produced a result not different from the uncorrected value. The standard error ( $S_b$ ) and 95% confidence limits for  $b$ ,  $r^2$ , and  $Sy \cdot x$  were calculated as indices of fit of the regression as recommended by Smith (1984).

## RESULTS AND DISCUSSION

The data collected from 24 species representing 11 spider families (Table 1) show much variation. The largest female is 112 times the smallest in the sample; number of eggs per clutch, egg diameter, and egg mass exhibit 39-, 2.8-, and 17.5-fold variation in these measures, respectively.

A good fit exists between egg mass and egg diameter (Fig. 1). The coefficient of determination ( $r^2$ ) is 0.99 and indicates the fraction of variation in egg mass explained by variation in egg diameter. The standard error of the estimate ( $Sy \cdot x$ ), standard error ( $s_b$ ) and 95% confidence limits for  $b$  are 0.035, 0.066, and 2.77-3.05, respectively. Support for the predictive ability of the model is provided by

Table 1.—Number, size, and mass of spider eggs. Data are averages ( $\pm$  SD).

FAMILY Species	Sample size (clutches)	Female live mass (mg)	Number of eggs per clutch	Egg diameter (mm)	Egg live mass (mg)
<b>FILISTATIDAE</b>					
<i>Filistata hibernalis</i>	14	347 (188)	129 (63)	1.37 (0.05)	1.42 (0.01)
<i>Physocyclus</i> species	3	28.9 (8.0)	73 (9.2)	0.82 (0.01)	0.31 (0.03)
<b>THERIDIIDAE</b>					
<i>Achaearanea tepidariorum</i>	5	37.7 (19.3)	149 (55)	0.59 (0.01)	0.12 (0.01)
<i>Argyrodes trigonum</i>	2	10.9	42	0.67	0.17
<i>Tidarren sisypoides</i>	1	51.8	238	0.66	0.16
<b>ARANEIDAE</b>					
<i>Acanthepeira stellata</i>	2	596	574	1.04	0.55
<i>Acanthepeira venusta</i>	5	182 (72)	232 (70)	0.88 (0.02)	0.34 (0.02)
<i>Argiope aurantia</i>	2	752	978	0.92	0.46
<i>Gasteracantha elipsoides</i>	1	175	195	0.81	0.25
<i>Mecynogea lemniscata</i>	7	59.9 (11.1)	25 (5.3)	1.01 (0.01)	0.54 (0.04)
<i>Metazygia wittfeldae</i>	5	87.0 (29.9)	84 (31)	1.06 (0.07)	0.51 (0.08)
<i>Nuctenea cornuta</i>	5	263 (52)	484 (130)	1.00 (0.02)	0.49 (0.05)
<b>AGELENIDAE</b>					
<i>Agelenopsis barrowsi</i>	1	138	60	0.98	0.47
<b>PISAUROIDAE</b>					
<i>Pisaurina mira</i>	3	293 (78)	264 (207)	1.15 (0.09)	0.78 (0.09)
<b>LYCOSIDAE</b>					
<i>Lycosa lenta</i>	6	1007 (234)	302 (48)	1.45 (0.05)	1.59 (0.15)
<b>OXYOPIDAE</b>					
<i>Peucetia viridans</i>	5	348 (22)	382 (36)	1.48 (0.02)	1.77 (0.08)
<b>SPARASSIDAE</b>					
<i>Heteropoda venatoria</i>	1	1221	184	1.66	2.10
<b>THOMISIDAE</b>					
<i>Misumenoides formosipes</i>	1	117	552	1.01	0.47
<i>Misumenops celer</i>	1	28.1	73	0.78	0.25
<b>SALTICIDAE</b>					
<i>Eris marginata</i>	1	43.1	59	0.93	0.37
<i>Phidippus audax</i>	4	223 (29.3)	186 (69)	1.26 (0.05)	1.03 (0.09)
<i>Phidippus pulcherrimus</i>	4	75.1 (9.0)	76 (15)	1.25 (0.01)	1.00 (0.08)
<i>Phidippus regius</i>	1	570	439	1.29	1.17
<i>Thiodina sylvana</i>	2	44.9	70	1.08	0.69

Wise's (1973) data on egg dimensions of *Linyphia marginata*. Given the reported diameter for these eggs, the equation (Fig. 1) predicts a wet weight equal to that indicated.

Although egg size exhibits much variation interspecifically (Table 1), I was impressed by the constancy of this measure within a species (see also Anderson 1978; Killebrew and Ford 1985). For example, the coefficients of variation involving egg diameter *within* each of the 12 species where multiple samples were available average 3.0% (Table 1). Conversely, the coefficient of variation for average egg diameter of the same 12 species is 24.3%. If egg size is species-dependent and not subject to environmental influences, egg sizes of the same species from different populations should not differ from one another. Such a comparison was made using the appropriate data from Kaston (1981) for Connecticut populations of seven species in common (Table 2). Analysis of the paired data indicate no significant differences exist ( $P = 0.94$ ) in egg size. The

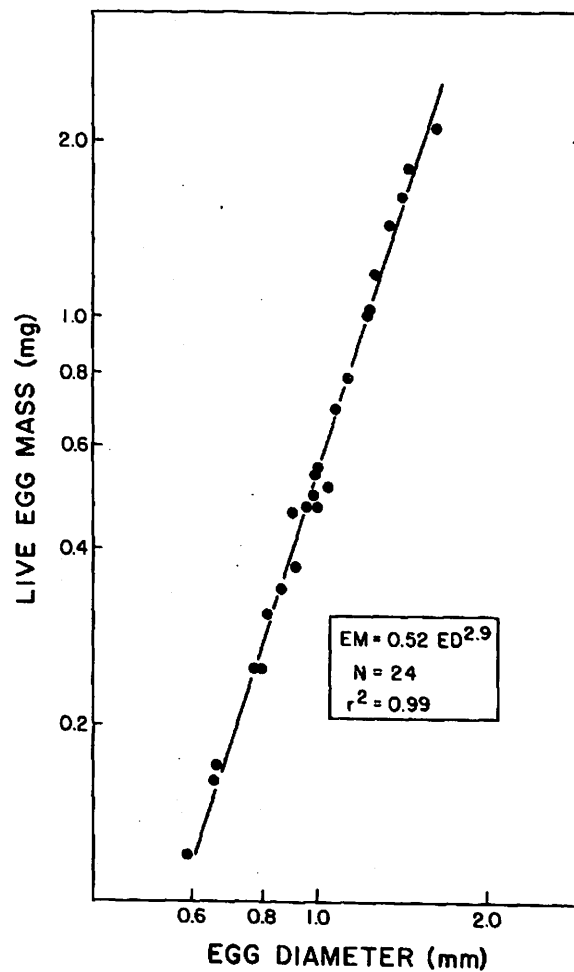


Figure 1.— Relationship between wet mass of egg (EM) and egg diameter (ED).

constancy of egg size provides validity to those studies comparing numbers of eggs or total egg mass as is so common in intraspecific studies.

The accuracy of estimates of the amount of energy incorporated into egg production made from number of clutches, number of eggs and their weight would depend on variation in energy density of eggs. Although variation in this measure is biologically significant and is correlated with the early life history patterns of individual species, the magnitude of this variation is not large (Anderson 1978). The reported values for the 12 species studied range from 26.3 to 29.0 joules per mg ash-free dry weight with an average of 27.3. Dry weight and

Table 2.—Comparison of egg size in spiders from Connecticut (Kaston 1981) and Florida (this study).

Species	Egg diameter (in mm)	
	Connecticut	Florida
<i>A. tepidariorum</i>	0.55	0.59
<i>A. trigonum</i>	0.65	0.67
<i>A. aurantia</i>	1.00	0.92
<i>N. cornuta</i>	1.00	1.15
<i>P. mira</i>	1.20	1.15
<i>M. formosipes</i>	0.96	1.01
<i>P. audax</i>	1.22	1.26

ash content of spider eggs are 31.9 and 3.58% of wet weight, respectively (Anderson 1978). Relative to the average, the potential error associated with the highest and lowest value are 6.2 and 3.7%, respectively. Since variation in the other variables such as number of clutches, number of eggs, and egg size is usually much larger, assuming a constant energy density would provide reasonably accurate comparative estimates of the energy incorporated into egg production in most cases. Certainly the number of egg sacs, number of eggs, and egg size can be counted and measured with ease and accuracy thus permitting more extensive studies of the energetics of reproductive output than would otherwise be practical.

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