Egg production and frequency of oviposition in *Achaearanea tepidariorum* (Araneae, Theridiidae)

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Introduction

The so-called "house spider" *(Achaearanea tepidariorum)* was first described as a species in the genus *Theridion* by Koch (1841), and it has been known by that name for over a century. Thus, the author of the taxonomic revision (Levi, 1955, p.2) considers it 'unfortunate that . . . one of the most common of our spiders, *Theridion tepidariorum,* must be placed in a different genus".

In Costa Rica, the species is one of the most abundant spiders associated with human dwellings and is apparently restricted to this habitat. It can be found on the inside and outside walls. Competitive exclusion is established with another common species, *Theridion rufipes* (Theridiidae), restricted to interior habitats. It follows that *A. tepidariorum* is found mainly on the outside walls of buildings where it competes with *Tidarren sisyphoides* (Theridiidae). Both species are extremely similar in size and body shape and are easily confused by the untrained eye. However, behaviourally and ecologically they are very different. *T. sisyphoides* prefers direct sunlight, while walls facing north or south, or otherwise protected from direct sunlight, are occupied mainly by *A. tepidariorum.* The webs of both are found under any salient structure on the wall, in the upper corners of window frames, and other similar situations.

Eggsac	A	B	C	D	E	F	G	H	I
1	197 (12)	173 (13)	350 (10)	316 (9)	220 (14)	210 (13)	203 (12)	163 (11)	228 (13)
2	202 (8)	169 (5)	233 (5)	207 (9)	109 (8)	334 (6)	208 (8)	158 (5)	116 (8)
3	153 (8)	152 (5)	105 (7)	287 (8)	197 (9)	301 (8)	160 (7)	140 (6)	205 (7)
4	153 (17)	206 (7)	302 (4)	183 (6)	130 (6)	263 (11)	158 (10)	196 (5)	137 (9)
5	79 (7)	144 (7)	260 (7)	309 (11)	135 (8)	579 (11)	85 (6)	133 (7)	143 (7)
6	337 (6)	195 (14)	389 (8)	230 (7)	120 (15)	636 (6)	340 (9)	183 (11)	127 (6)
7	144 (9)	104 (9)	343 (6)	181 (11)	165 (7)	465 (10)	151 (6)	94 (10)	173 (14)
8	412 (6)	78 (12)	289 (9)	321 (6)	228 (10)	352 (9)	418 (15)	67 (6)	235 (7)
9	186 (6)	249 (8)	400 (11)	419 (13)	254 (30)	297 (12)	191 (8)	237 (9)	262 (9)
10	221 (7)	325 (6)	342 (6)	508 (7)	251 (17)	148 (7)	228 (7)	315 (13)	258 (16)
11	283 (6)	221 (11)	332 (5)	55 (10)	189 (8)	228 (16)	289 (8)	210 (12)	197 (13)
12	327 (6)	201 (7)	275 (6)	440 (8)	87 (11)	382 (14)	332 (9)	189 (8)	
13	123 (19)	141 (13)	253 (10)	318 (12)	74 (7)	300 (20)	130 (11)		
14	61 (11)	136 (7)	250 (8)				186 (13)		
15		186 (13)	368 (13)				172 (10)		
16		152 (6)	125 (4)						
17			230 (9)						
18			323 (10)						
19			122 (8)						
20			254 (10)						
Total	2878 (128)	2832 (143)	5392 (156)	3774 (117)	2159 (150)	4495 (143)	3251 (139)	2085 (103)	2041 (109)
Average	205.57 (9.14)	177.00 (8.94)	269.60 (7.80)	290.31 (9.00)	166.08 (11.54)	345.77 (11.00)	216.73 (9.27)	173.75 (8.58)	185.55 (9.91)

Table 1: Ovipositing history of *A. tepidariorum* females (A – I). Number of eggs in each sac. Number of days since preceding sac (or since maturity for egg sac 1) in parentheses.

Material and Methods

Subadult female spiders were collected on the University of Costa Rica campus and fed until they moulted to maturity. A portion was kept virgin in an attempt to obtain unfertilized eggs. Others were brought into reproductive contact with males and their complete adult life histories were recorded (Valerio, 1970).

These females were fed regularly twice a week and each time were offered a prey item of approximately the same size. This procedure minimized fluctuations in the egg production due to the amount of food ingested. At meal time, every female was observed until the prey was subdued and wrapped.

A detail in the handling technique merits special comment. The containers were maintained with the door on the bottom. This saved a considerable amount of time and resulted in easier handling of the spiders. As the webs are built in the upper portion of the container, food or males can be introduced more easily through the door at the bottom and faeces can easily be removed. It would work the same for most web spinners.

Results and Discussion

The egg sacs hang near the horizontal support in the centre of the web, suspended by special silk threads. The female keeps in constant contact with the most recently built sac, using the tips of the first tarsi. Egg sac construction and other basic aspects of the biology of the species not discussed here have been extensively worked out by several investigators (Montgomery, 1903, 1906; Ewing, 1918; Bonnet, 1935). The female builds several sacs during her life, the number more commonly reported in the literature is from four to seven (all reports from temperate zones), and the world record is 17 sacs (Bonnet, 1935). In Costa Rica, an average of 14.11 sacs per female was found, with one female producing 20 sacs (Table 1).

Frequency of oviposition

The female builds its first sac some 12 days after reaching maturity, and subsequent sacs are built at intervals varying from four to 30 days (Table 1). The length of these intervals is undoubtedly affected by the amount of food ingested by the spider. An

Eggsac	A	B	C	D	E	F	G	H	I
1	12 (16.4)	13 (13.3)	10 (35.0)	9 (35.1)	14 (15.7)	13 (16.1)	12 (16.9)	11 (14.8)	13 (17.5)
2	20 (25.2)	18 (33.8)	15 (46.6)	18 (23.0)	22 (13.6)	19 (55.6)	20 (26.0)	16 (31.6)	21 (14.5)
3	28 (19.1)	23 (30.4)	22 (15.0)	26 (35.8)	31 (21.8)	27 (37.6)	27 (22.8)	22 (23.3)	28 (29.2)
4	45 (9.0)	30 (29.4)	26 (75.5)	32 (30.5)	37 (21.6)	38 (23.9)	37 (15.8)	27 (39.2)	37 (15.2)
5	52 (11.2)	37 (20.5)	33 (37.1)	43 (28.0)	45 (16.8)	49 (52.6)	43 (14.1)	34 (19.0)	44 (20.4)
6	58 (56.1)	51 (13.9)	41 (48.6)	50 (32.8)	60 (8.0)	55 (106.0)	52 (37.7)	45 (16.6)	50 (21.1)
7	67 (16.0)	60 (11.5)	47 (57.1)	61 (16.4)	67 (23.5)	65 (41.5)	58 (25.1)	55 (9.4)	64 (12.3)
8	73 (68.6)	72 (6.5)	56 (32.1)	67 (53.5)	77 (22.8)	74 (39.1)	73 (27.8)	61 (11.1)	71 (33.5)
9	79 (31.0)	80 (31.1)	67 (36.3)	80 (32.2)	107 (8.4)	86 (24.2)	81 (23.8)	70 (26.3)	80 (29.1)
10	86 (31.5)	86 (54.1)	73 (57.0)	87 (72.5)	124 (14.7)	93 (21.1)	88 (32.5)	83 (24.2)	96 (16.1)
11	92 (47.1)	97 (20.0)	78 (66.4)	97 (5.5)	132 (23.6)	109 (14.2)	96 (36.1)	95 (17.5)	109 (15.1)
12	98 (54.5)	104 (28.7)	84 (45.8)	105 (55.0)	143 (7.9)	123 (27.2)	105 (36.8)	103 (23.6)	
13	117 (6.4)	117 (10.8)	94 (25.3)	117 (26.5)	150 (10.5)	143 (15.0)	116 (11.8)		
14	128 (5.5)	124 (19.4)	102 (31.2)				129 (14.3)		
15		137 (14.3)	115 (28.3)				139 (17.2)		
16		143 (25.3)	119 (31.2)						
17			128 (25.5)						
18			138 (32.3)						
19			146 (15.2)						
20			156 (25.4)						

Table 2: Ovipositing history of *A. tepidariorum* females (A − I). Age of females at time of oviposition (in days) and estimated number of eggs produced per day in parentheses.

average of 6.67 days can be calculated from data presented by Montgomery (1906) from spiders fed ad libitum. The oviposition frequency was surprisingly regular in the nine females studied, no statistical differences in interval lengths could be detected at the 95% confidence level (t = 1.910 maximum, for female F). Although not statistically significant, there is a trend for the intervals between sacs to get longer as the female gets older (Table 3). This behaviour has been detected in other species (Bouillon and Lekie, 1961; Mikulska and Jacunski, 1968).

There is also no significant direct correlation between the length of the interval and the number of eggs per sac. However, it is considered that there must be some factors responsible for the observed variation in the number of eggs laid at the end of each interval that have not been detected by the statistical procedures used here (Fig. 1).

Number of Eggs per Sac

In this species the number of eggs in each sac seems to vary tremendously, from 27 (Ewing, 1918) to 477 (Bonnet, 1935). The upper limit is extended in the present report to 636 eggs in a single sac (Table 1, female F). A large part of this variation is apparently due to individual differences among the females.

The age of the female alone seems to have a minor effect on the number of eggs per sac. In other species there seems to be a normal negative correlation between egg production and age of female (Gertsch, 1949; Cazier and Mortenson, 1962).
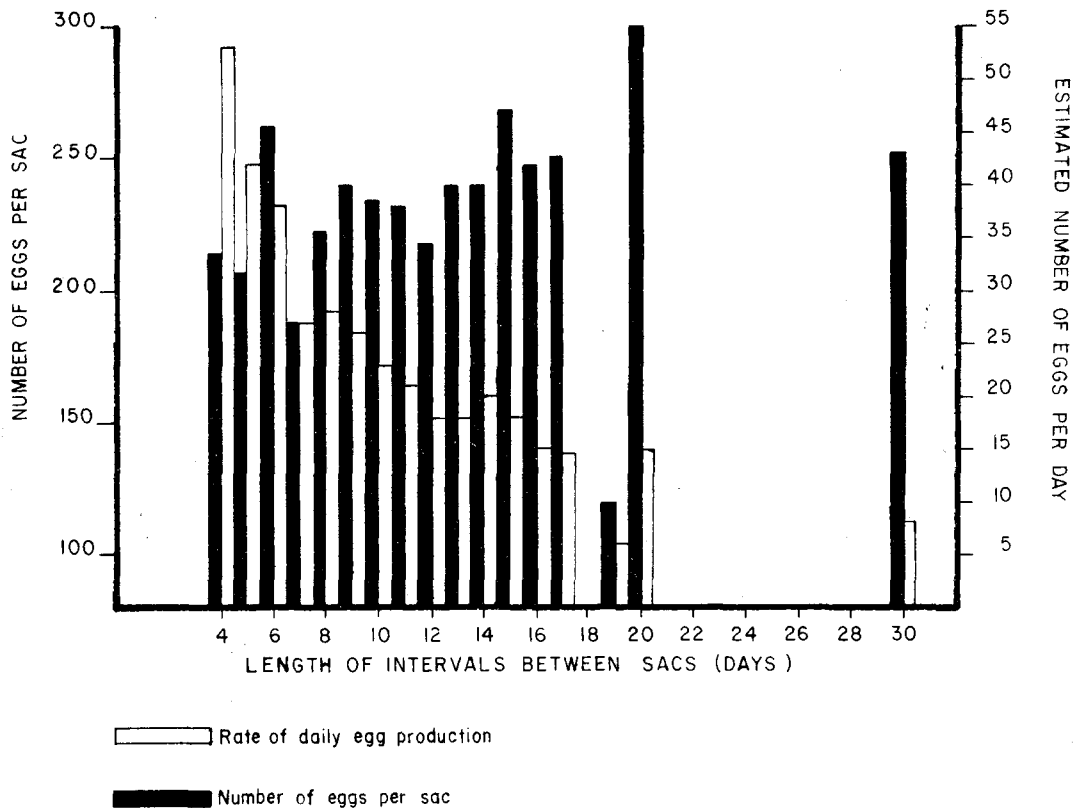

Fig. 1:   Effect of length of interval on the egg production. Data derived from Table 1.

Age (in days)	Number of Eggs per sac	Number of Eggs per day	Interval (In days)	Standard deviation of interval	n
0-9	316.0	35.1	9.00	(1 observation)	1
10-19	218.8	25.9	9.85	3.46	13
20-29	188.3	29.1	6.93	1.38	14
30-39	181.1	23.5	7.90	1.73	10
40-49	257.7	29.2	9.44	3.50	9
50-59	247.8	34.5	8.00	2.58	10
60-69	214.0	23.0	9.80	3.08	10
70-79	282.0	37.9	8.50	3.17	10
80-89	299.1	36.5	8.73	2.69	11
90-99	227.1	27.0	9.56	3.24	9
100-109	260.7	26.6	12.38	7.76	8
110-119	200.8	19.2	12.00	4.82	6
120-129	207.7	17.8	11.83	3.60	6
130-139	217.5	21.8	10.25	2.06	4
140-149	165.2	15.8	11.25	6.18	4
150-159	164.0	17.9	8.50	2.12	2

Table 3: Relation between age of female at oviposition, egg production and length of intervals between sacs. Average numbers, derived from Tables 1 and 2.

Age-Specific Reproductive Effort

Williams (1966) postulated that the intensity of reproductive effort (i.e., investment of energy by an individual in reproduction) should increase with age. As the possibility of surviving to future breeding time decreases (with age), a greater percentage of the energy budget is transferred to reproduction as an optimal strategy.

Field data collected by Clark (1970) on worm snakes, seem to support Williams' hypothesis. The system has been developed for vertebrates in which growth occurs during the reproductive life. Reproductive effort is measured as the weight of offspring relative to weight of the non-gravid female.

Numerical experiments have been planned to investigate this postulation, but with non-consistent results. Gadgil and Bossert (1970) concluded that the hypothesis is correct, but Fagen (1972) found that the opposite is true (i.e., reproductive effort decreases with age).

Although the system has not yet been applied to invertebrates it seems interesting to compare the effect of age on the reproductive effort in *A. tepidariorum*. Since this spider does not grow during its reproductive life, the absolute numbers of eggs produced (assuming a constant weight of the eggs) are a direct measure of this reproductive effort.

The energy put into reproduction increases at a slow rate as the female gets older (Table 3), in support of Williams' (1966) hypothesis. The trend continues until the female reaches the middle age (about 75 days), and then production drops favouring the opposite point of view (Fagen, 1972).

This problem illustrates the great risk of using theoretical mathematical models without first learning something about the behaviour and other aspects of the species in natural conditions.

Conclusions

Egg production and frequency of oviposition in this species seem to be regulated by several mechanisms acting independently:

1. The number of eggs in a sac depends in part on the length of the interval since the preceding sac, at least during the first part of adult life when intervals are somewhat shorter (Table 3 and Fig. 1), but egg production seems regulated by other factors.

2. Oviposition is probably related to the storage capacity of the female oviducts. Considering that a female produces some 24 eggs per day on the average

(Table 2) storage of eggs in the female body for more than 9 days (i.e. intervals longer than 9 days) would be highly selected against, since it would result in loss of reproductive time (a female cannot produce more eggs if her storage space is full, apparently about 220 eggs on the average).

3. The capacity of the oviducts seems to increase as the female gets older, since the length of the intersac interval rises a little during the first half of adult life (Table 3). After 75 days probably physiological wear of the reproductive structures due to age reduces the daily rate of egg production and still longer intervals are observed (Table 3). Additionally age probably causes a decrease in rate of silk production for sac spinning, thus influencing length of intervals.

4. There seem to be some ecological or behavioural factors, independent of egg production, which are capable of triggering egg sac construction and oviposition before the maximum storage capacity of the oviducts is reached. This idea is suggested by the presence of short intervals in females younger than 50 days, even though the daily rate of egg production is kept quite constant.

This behaviour might be correlated with factors affecting the amount of time necessary to produce the eggs, such as food scarcity and climatic conditions.

5. The age of the female affects egg production in such a way that is not detected by standard correlation tests, since its effect does not behave as a straight-line correlation. Table 3 shows an increasing egg production up to the middle adult life (75 days) and a clear decrease after that until death.

6. The data presented here suggest that two apparently conflicting mathematical models might not be exclusive of each other when applied to living systems (e.g., should reproductive effort increase or decrease with age?). The proportion in which two opposite tendencies are combined in nature probably represents part of the strategy set by a species, and a direct straight-line correlation in only one direction might be of rare occurrence.

Acknowledgments

References

BONNET, P. 1935: *Theridion tepidariorum* C. L. Koch araignée cosmopolite; repartition, cycle vital, moeurs. *Bull. Soc. Hist. nat. Toulouse* **68**: 335-386.

BOUILLON, A. and LEKIE, R. 1961: Cycle and rhythm in the ovulation of the spider *Latrodectus geometricus*. *Nature, Lond.* **191**: 620-621.

CAZIER, M. A. and MORTENSON, M. A. 1962: Analysis of the habitat, web design, cocoon and egg sacs of the tube weaving spider *Diguetia canities. Bull. Sth. Calif. Acad. Sci.* **61**(2): 65-88.

CLARK, D. R. 1970: Age-specific "reproductive effort" in the worm snake *Carphophis vermis. Trans. Kans. Acad. Sci.* **73**(1): 20-24.

EWING, H. E. 1918: The life and behavior of the house spider. *Proc. Iowa Acad. Sci.* **25**: 177-204.

FAGEN, R. M. 1972: An optimal life-history strategy in which reproductive effort decreases with age. *Am. Nat.* **106**(948): 258-261.

GADGIL, M. and BOSSERT, W. H. 1970: Life historical consequences of natural selection. *Am. Nat.* **104**: 1-24.

GERTSCH, W. J. 1949: *American spiders:* 1-285. D. Van Nostrand, New Jersey.

KOCH, C. L. 1841: *Die arachniden* **8**: 1-132, Nurnberg.

LEVI, H. W. 1955: The spider genera *Coressa* and *Achaearanea* in America North of Mexico (Aranea, Theridiidae). *Am. Mus. Novit.* **1718**: 1-33.

MIKULSKA, I. and JACUNSKI, L. 1968: Fecundity and reproduction activity of the spider *Tegenaria atrica* C. L. Koch. *Zoologica Pol.* **18**: 97-106.

MONTGOMERY, T. H. 1903: Studies on the habits of spiders, particularly those of the mating period. *Proc. Acad. nat. Sci. Philad.* **55**: 59-150.

MONTGOMERY, T. H. 1906: The oviposition, cocooning and hatching of an aranead *Theridion tepidariorum Biol. Bull. mar. biol. Lab.,* Woods Hole. **12**: 1-10.

VALERIO, C. E. 1970: Ability to store sperm by the female *Achaearanea tepidariorum* (C. L. Koch) (Araneae: Theridiidae). *Bull. Br. arachnol. Soc.* **1**: 88.

WILLIAMS, G. C. 1966: *Adaptation and natural selection:* 1-307. Princeton University Press, Princeton, N.J.