POPULATION DYNAMICS OF *TELENOMUS FARIAI* (HYMENOPTERA : SCELIONIDAE), A PARASITE OF CHAGAS' DISEASE VECTORS IX. LARVAL COMPETITION AND POPULATION SIZE REGULATION UNDER LABORATORY CONDITIONS

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INTRODUCTION

Telenomus fariai LIMA, 1927 is an endophagous egg parasite of several triatomine species, vectors of *Trypanosoma cruzi*, a protozoan responsible for Chagas' disease in Central and South America. This wasp has been reported to parasitize *Triatoma brasiliensis* (PELLEGRINO, 1950b), *Triatoma pallidipennis* (PELAEZ, 1944), *Triatoma sordida* (COSTA LIMA, 1928; MAZZA, 1942), *Triatoma infestans* (ABALOS and WYGODZINSKY, 1951; DREYFUS and BREUER, 1943, 1944; MAZZA and JÖRG, 1938; PELLEGRINO, 1950a; PINTO, 1942), *Triatoma maculata* (PELLEGRINO, 1950b), *Triatoma megista* (=*Panstrongylus megistus*) (COSTA LIMA, 1927 ; PELLEGRINO, 1950a), *Triatoma phyllosoma* (ZELEDÓN, 1957; RABINOVICH, 1971), *Triatoma vitticeps* (PELLEGRINO, 1950b), *Triatoma dimidiata* (ZELEDÓN, 1957 ; ZELEDÓN *et al.*, 1965), *Triatoma rubrovaria* (PELLEGRINO, 1950b), and *Panstrongylus chinai* (ZELEDÓN, 1957).

At 28°C the free living adults have a longevity of about 2-3 days if females, and about one day if males. Each female is able to parasitize about 10 hosts per day during their lifespan, and lays 6-8 eggs in a single host. Development to the adult takes about 23-24 days at 28°C. Normally 6-7 adults emerge, being none, or at the most one of them, a male. If a male is present, copulation takes place inside the host or immediately after emergence. Sex determination is arrhenotokous. However, all females, fertilized or not, are sexually mature, and start searching for hosts as soon as they emerge.

A certain variability in the number of emerging adults per host has been recorded, but this seems clearly related to the size and/or species of host eggs. For example, 11.3, 7.8, 6.5, 6.7, and 4.1 adults per host have been reported from *T. phyllosoma*, *T. dimidiata*, *P. chinai*, *T. megista*, and *T. sordida*, which have eggs of decreasing size, respectively (ZELEDÓN, 1957; COSTA LIMA 1927; 1928). However, RABINOVICH (1971) determined that older larval or pupae mortality could not account for a remarkable constancy in the parasite progeny per host, when only one host species was used; it was suggested that young larvae mortality may be playing a key role

in progeny constancy, but no data were available to support this hypothesis.

On the other hand, occasional observations from the field and the laboratory indicate that competition for limiting resources may occur. This is suggested not only by a larger than average number of adults emerging per host, but also by double number of males per host, for the same host species (BOSQUE and RABINOVICH, 1978). This paper had as objectives to determine if this competition occurs, and if so, which might be the density-dependent mechanism to account for the constancy in progeny production per host.

MATERIALS AND METHODS

The parasite population was originally from Costa Rica, but had been reared in the laboratory for 3 years. All parasite stocks were maintained in 9.5×5cm cotton-plugged glass vials. No food or water was used for, when offered it did not increase longevity or reproductive capacity. The host population was *Triatoma phyllosoma pallidipennis*, from Mexico, and had been reared in the laboratory for many years. They were kept in 3.7 liter jars, and fed weekly on chicken for one hour. Both parasites and host were kept in a climatic room at $28\pm1°C$ and $60\pm5\%$ RH.

The parasite and host stocks were checked daily to separate the host's eggs and newly emerged wasps; only 0-24 hour host eggs and 0-24 hour adult female wasps were used in the experiments. The experiments were carried out in the same parasite stock's glass vials, where a given number of female wasps were offered five hosts. Eight different parasite densities were used: 1, 3, 5, 10, 20, 30, 40 and 50 parasites per vial. As recording the number of progeny per host in each development day implied dissecting and killing both host and parasites, each parasite density was replicated 72 times, in order to obtain 3 replicates for each of the 24 days of development.

The five hosts were left in contact with the wasps for 24 hours ; the only exception was a set of 3 replicates in which the wasps were in contact with the hosts for only 3 hours (called development day 0.13), in order to check the number of eggs laid (the parasite's eggs hatch few hours after being laid). After being used in the experiments the wasps were not used any more for experimental purposes, and were returned to the stock vials. In total the 72 replicates for each density required setting up 576 experimental vials, which used 2,880 host eggs, and 11,448 female wasps.

For development days 0.13, 1 and 2, when wasp eggs and very small larvae are present, the host eggs were left in a 5 : 1 : 1 acetic acid-menthanol-chloroform solution for 2-3 hours, to soften the chorion. Then, using a pair of entomological needles, the eggs were dissected, and their contents coloured with methylen blue; the material was extended on a slide and eggs and/or larvae counted under a stereoscope. For development days 3 and older, the host eggs were preserved in 10% formalin until

dissection, and staining was not required. The length and width of every host egg was measured, and the following information of its contents was recorded:

1. the number of wasp eggs
2. the number of larvae, and the length and width of each (if aged 3 days or more);
3. the number, sex, and length of pupae or adults.

For both host eggs and larvae, the length and width were used to calculate their volume, assuming that the bodies were elipsoidal; the volume formula used was $V = 4/3\pi ab^2$, where a and b are the major and minor elipsoid semiaxes, respectively.

RESULTS

Tables 1-4 show the number of larvae, pupae, adults and total progeny per host, for each development day, and each density. The drastic decrease of larvae around the 10th day of development (Table 1) indicates the initiation of pupation, as can be

Table 1. Number of larvae per host. m=mean, DS=standard deviation. Sample size is five hosts.

Day of Development	Parental Density															
	1		3		5		10		20		30		40		50	
	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS
0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1	6.86	1.81	14.30	2.50	12.40	0.92	26.73	2.04	36.68	2.44	46.87	4.30	51.93	4.75	—	—
2	5.33	0.75	11.10	4.87	21.13	2.64	25.60	1.90	35.07	3.56	31.20	1.39	29.20	6.60	—	—
3	6.39	1.79	14.39	1.96	12.73	1.85	20.53	3.64	21.20	2.79	16.23	0.37	21.00	1.44	21.26	1.94
4	7.26	1.20	11.06	0.41	13.06	0.23	16.18	2.14	16.46	2.80	15.73	0.46	17.13	1.85	14.99	0.72
5	6.89	0.95	11.53	1.67	13.26	0.75	15.60	1.38	13.86	1.20	12.33	1.85	18.39	3.60	14.73	0.30
6	7.36	0.15	10.99	2.90	12.33	1.60	14.69	0.43	16.60	0.87	11.79	0.80	19.60	1.21	12.86	1.33
7	6.08	0.36	12.19	0.87	13.06	2.13	15.73	1.41	15.93	0.70	12.46	0.61	16.06	0.23	15.13	1.70
8	6.88	1.83	10.86	1.28	13.33	2.72	11.19	1.00	15.53	0.90	14.66	2.80	14.59	1.50	14.93	0.98
9	7.59	0.37	11.26	0.83	11.93	1.55	15.79	0.52	14.06	0.61	15.73	0.92	15.79	1.05	15.20	0.52
10	7.14	1.97	11.33	2.46	12.46	1.22	9.99	3.01	16.13	1.85	13.53	1.67	15.23	0.25	13.66	0.75
11	3.75	1.39	7.39	0.79	0.73	0.94	5.39	2.25	5.80	3.67	14.53	2.23	11.58	2.74	12.60	1.77
12	1.73	1.13	3.39	3.93	6.93	1.02	1.93	1.50	2.73	0.70	14.13	0.92	15.19	4.01	8.39	1.56
13	2.24	1.23	1.06	0.83	0.93	0.94	2.66	1.17	6.06	3.05	12.13	3.05	9.93	5.71	8.79	1.92
14	0.46	0.64	1.53	1.33	0.79	1.38	1.20	0.34	0.66	0.23	0.99	0.40	10.00	1.90	9.60	0.87
15	1.46	2.36	2.73	2.77	1.20	0.87	1.26	1.85	0.79	0.52	5.26	0.80	7.06	4.00	4.26	1.81
16	1.26	1.13	1.33	0.80	0.53	0.61	1.15	1.60	3.26	2.33	7.39	2.02	2.46	1.81	7.13	1.92
17	0.86	0.61	2.20	2.30	8.46	2.80	2.73	2.33	5.39	2.55	9.39	3.98	5.53	1.33	4.13	3.06
18	0.93	0.70	1.33	1.17	0.19	0.19	0.46	0.30	4.33	2.33	1.86	1.10	4.19	1.77	4.19	2.35
19	0.59	0.69	0.19	0.19	0.26	0.23	0.26	0.23	5.96	1.96	10.06	2.30	3.86	3.28	6.79	3.30
20	1.40	1.44	3.53	1.30	0.46	0.64	3.06	0.94	2.93	0.80	0.99	0.34	1.93	1.41	7.19	3.21
21	0.06	0.11	0.06	0.11	0.73	1.10	0.39	0.39	3.13	1.92	4.66	2.96	5.39	1.50	6.93	0.30
22	0.13	0.11	0.79	0.87	1.20	1.39	4.33	2.85	2.59	1.90	4.80	1.99	4.19	1.74	7.59	1.73
23	0.00	0.00	0.93	1.44	0.46	0.50	0.26	0.11	4.66	2.19	5.53	4.40	4.66	0.11	5.61	1.37

Table 2. Number of pupae per host. m, DS and sample size as in Table 1.

Day of Develop- ment	Parental Density															
	1		3		5		10		20		30		40		50	
	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS
9	0.73	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	1.33	2.30	0.00	0.00	0.00	0.00	5.46	2.90	0.00	0.00	0.13	0.11	0.00	0.00	0.33	0.57
11	4.81	2.33	4.26	0.98	12.39	2.55	8.59	5.60	11.66	3.49	0.00	0.00	1.66	1.47	3.06	1.22
12	6.05	2.08	8.79	5.17	6.66	1.67	13.13	2.01	13.26	0.57	0.00	0.00	1.66	1.70	5.00	0.60
13	4.26	1.10	10.73	1.40	10.79	1.83	12.73	0.50	9.53	3.33	2.13	3.18	6.26	4.80	3.53	1.97
14	7.79	1.11	10.26	1.33	11.66	1.72	14.99	0.91	15.86	1.62	16.39	2.30	5.73	2.01	4.79	0.20
15	6.33	2.38	7.86	3.70	10.86	1.70	14.06	2.30	15.39	1.90	10.79	2.08	8.33	3.91	10.99	2.90
16	6.19	1.21	9.53	1.81	10.53	0.80	14.56	1.70	13.53	2.11	5.99	2.30	13.79	3.99	8.13	5.52
17	6.39	1.77	8.51	2.07	4.06	1.81	11.46	3.62	3.66	2.04	5.00	3.36	7.13	3.02	7.46	3.28
18	6.79	1.60	7.79	4.80	12.86	1.61	15.46	0.80	2.99	1.31	9.79	2.30	10.93	3.92	1.86	1.20
19	6.73	1.85	5.26	2.65	10.93	4.62	1.06	1.50	2.59	2.35	4.26	3.41	11.66	4.30	1.53	0.98
20	3.46	0.83	1.46	0.94	1.46	1.67	3.66	1.79	5.86	5.19	2.33	1.70	3.06	2.68	0.46	0.23
21	0.73	0.75	1.66	1.61	0.06	0.11	0.39	0.34	4.73	1.67	3.99	2.98	1.66	2.02	0.79	0.60
22	0.06	0.11	0.66	0.93	0.26	0.23	0.39	0.19	1.26	1.51	1.46	1.00	0.46	0.41	0.19	0.00
23	0.13	0.23	0.79	1.03	0.06	0.11	0.33	0.11	1.59	1.21	1.20	1.56	0.46	0.11	0.39	0.52

Table 3. Number of adults per host. m, DS and sample size as in Table 1.

Day of Develop- ment	Parental Density															
	1		3		5		10		20		30		40		50	
	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS
18	0	0	0.93	1.61	0	0	0	0	8.93	2.11	3.93	4.74	0	0	7.33	1.41
19	1.13	0.98	3.11	4.04	2.33	4.04	13.59	3.74	9.08	3.94	0	0	0	0	6.80	3.46
20	2.79	1.05	6.13	2.02	12.33	3.10	9.06	2.44	5.60	5.70	13.53	2.83	7.59	3.60	5.93	4.20
21	7.26	0.23	8.60	2.64	10.79	0.60	13.33	1.30	5.19	1.44	4.93	2.10	5.46	3.97	6.06	1.70
22	7.19	0.20	10.39	1.44	11.66	3.00	11.66	2.51	11.86	1.61	7.46	1.70	8.26	1.47	4.04	2.48
23	7.66	0.80	10.53	0.83	13.66	0.90	12.66	0.92	8.66	1.10	6.13	3.51	8.73	1.70	8.14	1.53

verified by the increasing number of pupae (Table 2); a similar change can be observed around development day 20, when pupae become adults (Table 3). In Table 4, at development day 0.13, the mean number of eggs per host is given.

To evaluate the effect of density it seemed better to eliminate first the variation in age dependent survival, typical of sequentially sacrificed replicated experiments (BRYANT and SOKAL, 1967), in which some development days show a number of surviving individual larger than in a previous day. This was obtained by smoothing, for each density, the values of the time series by the following procedure: (a) plotting the mean and one standard deviation for the series; (b) drawing a line through the plotted points on condition that (i) it should be within the one standard deviation

Table 4. Total progeny per host. m, DS and sample size as in Table 1.
For development day 0.13 the progeny is composed exclusively of eggs.

Day of Develop-ment	Parental Density														
	1		3		5		10		20		30		40		50	
	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS	m	DS
0.13	6.60	1.31	16.50	1.40	15.93	1.21	29.9	2.45	30.80	4.85	61.47	10.43	55.2	7.7	—	—
1	6.86	1.81	14.30	2.50	12.40	0.92	26.73	2.04	36.68	2.44	46.87	4.30	51.93	4.75		
2	5.33	0.75	11.10	4.87	21.13	2.64	25.60	1.90	35.07	3.56	31.20	1.39	29.20	6.60	—	—
3	6.39	1.79	14.39	1.06	12.73	1.85	20.53	3.64	21.20	2.79	16.23	0.37	21.00	1.44	21.26	1.94
4	7.26	1.20	11.06	0.41	13.06	0.23	16.18	2.14	16.46	2.80	15.73	0.46	17.13	1.85	14.99	0.72
5	6.89	0.95	11.53	1.67	13.26	0.75	15.60	1.38	13.86	1.20	12.33	1.85	18.39	3.6	14.73	0.30
6	7.35	0.15	10.99	2.90	12.33	1.60	14.69	0.43	16.60	0.87	11.79	0.80	19.60	1.21	12.86	1.33
7	6.08	0.36	12.19	0.87	13.06	2.13	15.73	1.41	15.93	0.70	12.46	0.61	16.06	0.23	15.20	1.79
8	6.88	1.83	10.86	1.28	13.33	2.72	11.19	1.00	15.33	0.90	14.66	2.80	14.59	1.50	14.93	0.98
9	8.33	0.41	11.26	0.83	11.93	1.55	15.79	0.52	14.06	0.61	15.73	0.92	15.79	1.05	15.20	0.52
10	8.48	1.28	11.33	2.46	12.46	1.22	15.46	0.41	16.13	1.85	13.66	1.61	15.23	0.23	13.99	1.11
11	8.56	1.09	11.66	0.57	13.13	0.61	13.99	3.36	17.46	0.57	14.53	2.23	13.24	1.30	15.66	0.98
12	7.78	1.26	12.20	1.31	13.60	0.79	15.06	0.57	15.99	0.40	14.13	0.92	16.86	2.33	13.39	2.08
13	6.51	0.26	11.79	1.05	11.73	1.10	15.39	1.24	15.60	0.39	14.26	1.33	16.20	3.17	12.33	0.11
14	8.26	0.64	11.79	0.20	12.46	0.64	16.20	0.69	16.53	1.85	17.39	2.10	15.73	0.11	14.39	0.87
15	7.8	0.19	10.6	1.44	12.06	0.83	15.33	0.50	16.20	1.44	16.06	1.33	15.39	0.72	15.26	1.28
16	7.46	0.41	10.86	2.54	11.06	0.30	15.71	0.10	16.79	1.21	13.39	0.34	16.26	2.19	15.26	3.69
17	7.26	1.27	10.71	1.92	12.53	2.20	14.19	1.56	15.86	1.90	14.39	0.91	12.66	1.70	13.99	1.20
18	7.73	0.61	10.06	2.33	13.06	1.50	15.93	1.00	16.26	1.10	15.60	1.56	15.13	2.20	13.39	1.11
19	8.46	0.46	12.46	0.30	13.53	0.46	14.93	2.13	17.65	2.40	14.33	1.70	15.53	1.02	15.13	0.80
20	7.76	0.23	11.13	0.30	14.26	1.02	15.79	1.74	14.39	1.11	16.86	1.33	12.60	0.87	13.60	1.50
21	8.06	0.90	10.33	0.98	11.60	0.60	14.13	0.98	13.06	1.36	13.60	0.91	12.53	1.72	13.79	1.05
22	7.39	0.20	11.86	0.50	13.13	1.51	16.39	0.79	15.73	0.80	13.73	0.70	12.93	1.81	11.86	0.75
23	7.79	0.60	12.26	0.61	14.19	0.69	13.26	1.33	14.93	1.33	12.86	0.90	13.86	1.60	14.16	0.49

band, (ii) every value should be equal or less than a previous value, and (iii) all original data points should be preserved where possible. The results of the smoothing procedures, expressed as survivorship curves, show that there is a marked decrease in survivorship with density, particularly during the first few days of larval development (Fig. 1).

The difference between the number of newly hatched larvae and pupae, and the difference between the number of pupae and adults, provide an estimate of total larval and pupal mortality, as a function of density (Fig. 2). The former shows a continuously increasing value, while the latter decreases after density 30. This suggests that if larval mortality is above 60%, then the surviving larvae have a better chance of surviving as pupae.

As the number of emerging adults belong to a new generation, the density effect can also be analyzed as a stock-recruitment curve (RICKER, 1954). This curve shows an intersection with the 45° line near a population size of 13 (Fig. 3), indicating that,
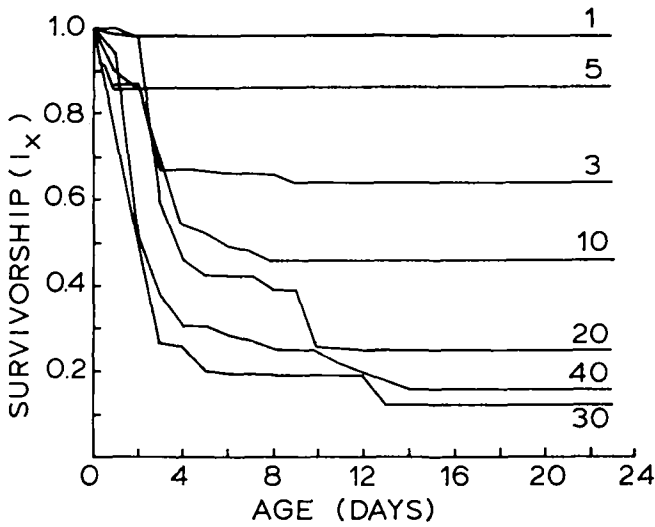
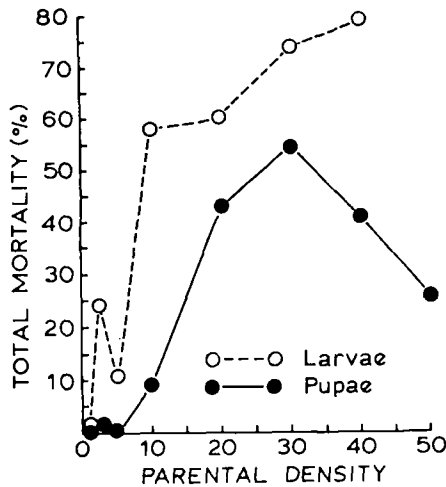Fig. 1. Survivorship curves for progeny of *Telenomus fariai* at different parental densities.

Fig. 2. Total larval and pupal mortality of *T. fariai* as a function of parental density.

with the resources available (five hosts), a stable population of 13 wasps would eventually be achieved. Such a reproduction curve suggests a very efficient population regulation mechanism. In order to determine at what stage of the life cycle the mechanism is in operation, MORRIS' regression method was applied (MORRIS, 1959, 1963a, b).

MORRIS' technique to test within-generation density dependence survival was selected because, being a controlled experimental situation, there is no sampling error in density estimates. Thus, as shown by KUNO (1971), the bias of MORRIS' method
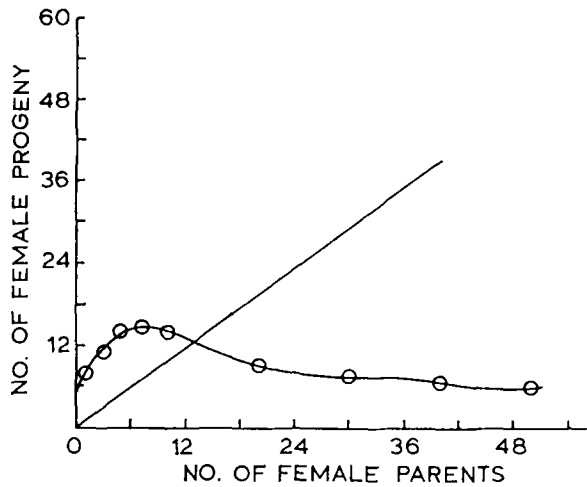
Fig. 3. Stock-recruitment curve of *Telenomus fariai*.
The 45° line represents the parent-progeny relationship
that will produce a stable population.
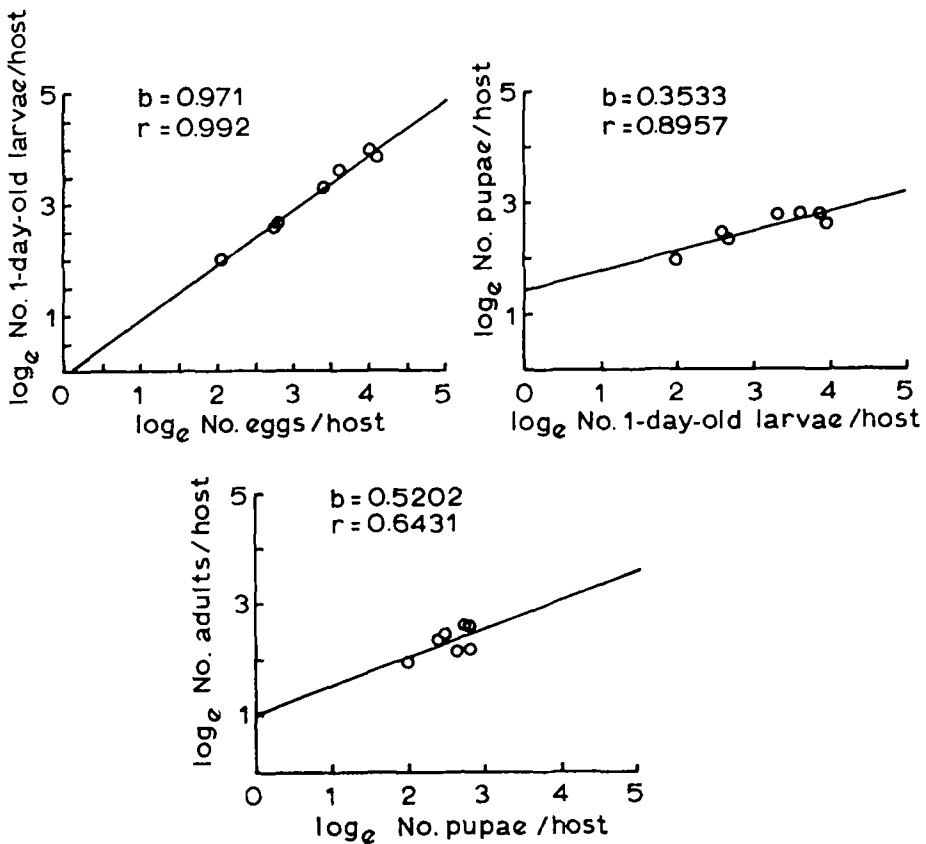
Fig. 4. Results of applying MORRIS' regression technique to within-generation,
between-stages survival. Testing slope deviation from $b=1$ with the t test, only
the larva-pupa relationship deviated at a statistically significant level of 5%.

by incorrectly including some relation as density dependent when they are not, is negligible. PETERMAN (1978) gives a review of the limitations of this method and of the alterantive one by VARLEY and GRADWELL (1963, 1968).

The regression of the natural logarithms of the number of individuals in one stage and the next, is shown in Fig. 4 for the egg, larval, pupal and adult stages. Of the three regressions, only the larval-pupal one shows a slope value significantly different from 1 (*t* test, 5% level), indicating that the density dependence seems to be operating significantly only during the larval period.

A similar procedure was applied between each developmental day, in order to determine which of the larval ages seemed more critically affected by density. Figure 5 shows the values of the slope and its 95% confidence band; despite some very low values (particularly in the 10th day of development) the standard errors are such that only larvae of 1, 2, and 3 days old prove to have significant density dependence.

Although the precise mechanism of action of the larval competition process was not studied, no cases of aggression (for example, marks of an attack with the mandibles) were observed; thus, probably either accidental damage, suffocation, or lack of food would account for mortality at this stage, as it occurs in many other gregarious parasites (SALT, 1961; FISHER, 1963). Of these we are inclined to think that lack of food might be the dominant mechanism for it was observed that average larval size decreased singnificantly as density increases (Fig. 6).
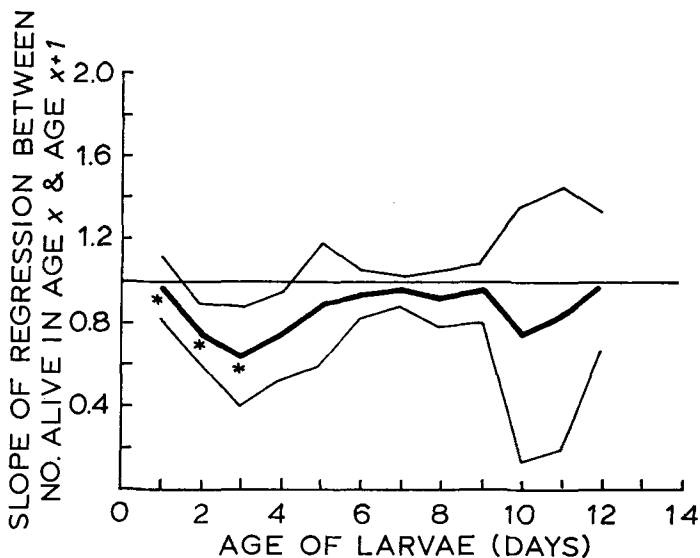

Fig. 5. Results of applying MORRIS' regression technique to within-larval stage, between-development day survival. Each slope value results from regressing the corresponding development day in the horizontal axis and the next. Asterisks identify the statistically significant deviations from $b=1$ at the 5% level. Thick line: slope values; thin lines: 95% confidence band.
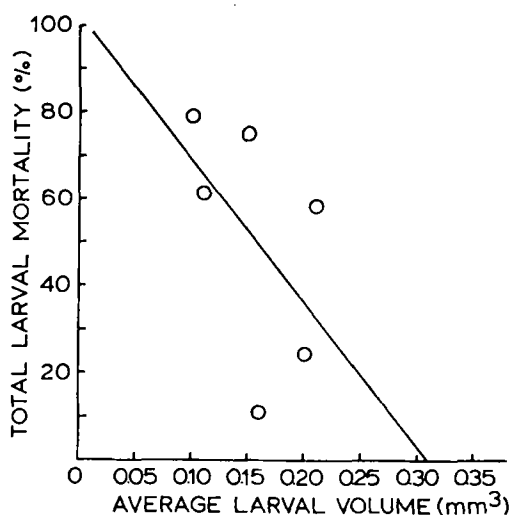
Fig. 6. Relationship between total pupal mortality and average larval volume. Each data point corresponds to a parental density. Density 50 was not used because wasp eggs and day 1 larvae were not counted.

DISCUSSION

These experiments suggest that scrambling for resources by the progeny of *Telenomus fariai* could occur. As density increases, the number of parasite eggs laid per host also increases (a record of 95 eggs in one host was found at density 30, compared with the average of 7.9 eggs at density 1). This leads to a situation where the number of larvae per host is larger than can be supported by the host's resources. The competition seems strongest between the second and fourth day of larval development, and is relatively efficient, stabilizing the parasite population at a level of about 13 wasps per 5 hosts.

However, it is not known whether such competition could be important in field populations. BOSQUE and RABINOVICH (1978) have shown that *T. fariai* females leave a mark on each host after oviposition; this mark is usually respected by other searching females who, after antennal inspection, leave the host without attempting to oviposit. Simple interference probably prevents this behavior from operating under these critically crowded laboratory density levels, where up to five females were seen ovipositing on a host simultaneously.

However, although very little is known about the field ecology of *T. fariai* occasional cases of multiparasitism have been recorded (COSTA LIMA, 1928; LUMBRERAS *et al.*, 1955; PELAEZ, 1944; PELLEGRINO, 1950; ZELEDÓN *et al.*, 1965). Several factors may play a role in leading to a situation where significant scramble competition might occur under natural conditions: (1) the marks will *not* be respected if the searching female has never oviposited before (BOSQUE and RABINOVICH, 1978); (2)

the host's egg laying capacity is fully dependent on a blood meal, after which an extremely sedentary behavior is dominant, thus producing most of its eggs in a relatively short radius (such a contagious distribution tends to produce higher *effective* parasite densities); (3) the parasites seem to have the ability to find well hidden host's eggs, thus suggesting some guiding (probably olfactory) mechanism to make their search more efficient; and (4) the dispersal capacity of adult females seems extremely low.

Other factors may reduce the probability of resource competition. The parasites show a marked positive phototropism, and as the hosts are usually hidden in dark places, this may "dilute" the effective population; and the adults have a very short adult lifespan (an average female can only parasitize about 10 hosts per day, and lives around 2-3 days). At present, the role of larval competition, as a regulation mechanism in *Telenomus fariai* field populations is poorly understood and should be investigated.

SUMMARY

A series of experiments were carried out with the endophagous egg parasite *Telenomus fariai* on its host *Triatoma phyllosoma pallidipennis* to determine the possible role of intraspecific competition by the parasite progeny in population regulation of the parasite. Eight parasite densities (1, 3, 5, 10, 20, 30, 40, and 50 individuals per vial) were used, and the design of sequentially sacrificed replicates applied. Survivorship curves for each density indicated smaller number of progeny per host at higher densities, and the shapes of the curves suggested a relatively early mortality process. MORRIS' linear regression technique for determining within-generation density-dependence was used, and the results showed that only larval mortality could be identified as density dependent. The same technique applied within the larval stage proved that only mortality of larvae in their second, third, and fourth day of development were responsible for population regulation. The applicability of the technique, as well as the relevance of the results for natural population, is discussed.

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シャガス病の媒介昆虫の卵寄生蜂 *Telenomus fariai* の
個体群動態 IX. 実験条件下での幼虫の競争と個体数調節

G. ESCALANTE・J. E. RABINOVICH

実験はシャガス病を媒介するサシガメの1種 *Triatoma phyllosoma* の卵を寄主として行なった。蜂の成虫を，数を8段階にかえて放し以後次世代成虫が羽化するまでの寄主内での発育段階別生存数の推移を調べ，生存曲線を比較した。高密度条件では寄主あたり次世代成虫数は減少し，これは比較的初期の死亡過程によることが示唆された。実際に，MORRIS の回帰法で調べたところでは，密度依存的と判定されたのは幼虫期の初期の死亡過程のみであった。自然個体群との関連でのこれらの結果の意義について論じた。