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Population dynamics of Telenomus fariai (Hymenoptera: Scelionidae), a parasite of Chagas' disease vectors. V. Parasite size and vital space

by

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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* (11), *T. pallidipennis* (9), *T. sordida* (6, 7), *T. infestans* (1, 2, 3, 8, 10, 12), *T. maculata* (11), *T. megista* (= *Panstrongylus megistus*) (5, 10), *T. phyllosoma* (15), *T. vitticeps* (11), *T. dimidiata* (15, 16), *T. rubrovaria* (11), and *Panstrongylus chinai* (15).

The number of wasps emerging per host egg and their size vary when parasitism takes place in different host species. There is an argument as to whether variation in parasite size is a product of host egg volume or of the number of parasites produced per host egg. ZELEDÓN (15) very clearly shows the relation between the egg volume of three different hosts and progeny number/host egg, but he does not relate his conclusions to parasite size. On the other hand, DREYFUS and BREUER (3) show a strong correlation between the number of adults emerged/host egg and parasite size, but disregard the possible effect of host egg volume. It is the intention of this paper to elucidate the relationship between host egg volume, parasite size, and progeny production per host egg.

MATERIAL AND METHODS

To avoid possible unknown nutritional effects resulting from the use of different species as hosts, and due to the fact that within one species, host egg volume shows a certain degree of variability, these experiments were performed

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using only one host species, *Triatoma phyllosoma pallidipennis.* Parasites were from a population originally from Costa Rica, that had been reared in the laboratory for about 10 generations. The host population was obtained from the School of Biology of the Central University of Venezuela, where it has been reared for several years.

Both adult wasps and hosts were kept in a climatic room at 28 ± 1 C and 60 ± 5 % relative humidity. Adult *T. phyllosoma pallidipennis* were maintained in 3.8 liter jars, and fed weekly. Eggs were collected from these jars every 24 hours and kept in labeled and dated vials. Adult wasps were kept in small (1.5 x 5.0 cm) cotton-plugged glass vials. No food or water was needed for their normal activity. Parasitized eggs, isolated in vials, were checked daily for emergence in order to determine the wasps' ages. To avoid possible age specific differences in behavior and fecundity, all wasps used were newly emerged individuals (0-24 hr).

The experiment was performed in a climatic chamber at 24 ± 1 C and 60-90 % relative humidity. One newly emerged female parasite was placed in a cotton-plugged glass vial for 24 hours with one 0-24 hr old host egg. This procedure was repeated 160 times on several successive days. After 24 hours had elapsed, parasites were killed and host eggs kept under observation in individual vials at 28 C until the parasite progeny emerged.

The emerged wasps were counted, sexed, and their body length measured. The major and minor axes of the host egg were also measured in order to estimate its volume by the formula of a prolate spheroid (formed by the rotation of an ellipse about its major axis), given by $4/3\ \pi\ ab^2$, where a and b are the major and minor semiaxes, respectively. After it was measured, the host egg was dissected to count, sex, and measure dead adults, if any, and to count dead larvae or pupae that sometimes constituted the remains of an evacuated host egg.

Hereafter, total production per host egg will mean total number of individuals per host egg, i.e., emerged adults + dead adults + dead pupae + dead larvae; total number of adults will mean emerged + dead adults, and similarly for total number of males and females per host egg.

RESULTS

PROGENY PRODUCTION PER HOST EGG: From the total number of repetitions (160), 8 had dead parasites after 24 hr. As it was impossible to determine the exact time of death, these replicates were discarded. For the remaining 152 replicates, Table 1 summarizes the statistics on progeny production per host egg. The mean number of adults emerged per host egg is lower than the one reported by ZELEDÓN (15) for *Telenomus fariai* using *Triatoma phyllosoma* as host. In Table 2 the mean number of emerged adults per host egg for different host species is represented with its source; in one instance (LIMA, 6), mean values were computed from the author's original data. Host egg volume estimates for these species were not available, with one exception (15), where the estimates were 2.022, 1.457, and 1.266 mm^3 for *T. phyllosoma*, *T. dimidiata*, and *P. chinai*, respectively. It is also known that the eggs of *T. megista* are larger than those of *T. sordida*. In all these cases we can observe a clear trend towards a larger number of parasites emerged per host egg for larger host eggs.

TABLE 1

Statistics of progeny production per host egg from 152 replicates

	Total Production	Emerged Adults	Total Females	Emerged Females	Total Males	Emerged Males
Mean	8.2	7.4	6.6	6.4	1.0	1.0
Range	5-14	0-13	0-11	0-11	0-5	0-5
SD	1.3	1.4	2.0	2.1	0.5	0.6

TABLE 2

Progeny production per host egg from different host species

Species	Mean N° of adults emerged/host egg	Source
Triatoma phyllosoma	11.34	ZELEDÓN, 15
T. pallidipennis	9.21	PELÁEZ, 9
T. dimidiata	7.81	ZELEDÓN, 15
T. phyllosoma pallidipennis	7.40	Present study
T. infestans	7.05	DREYFUS & BREUER, 5
T. megista	6.73	LIMA, 6
Panstrongylus chinai	6.53	ZELEDÓN, 15
T. brasiliensis	5.86	PELLEGRINO, 11
T. vitticeps	4.57	PELLEGRINO, 11
T. maculata	4.18	PELLEGRINO, 11
T. sordida	4.12	LIMA, 6

EVALUATION OF LATE MORTALITY: It has already been reported that in some cases parasites do not complete their development but remain inside the host eggs as larvae, pupae, or adults (6, 9, 11). However, no quantitative account of this fact has been published. By comparing the first two columns of

Table 1, one obtains an indication of the degree of mortality during the late stages of development (last instar larvae and pupae). Although the number of eggs deposited by female parasites was not counted, it is known that it greatly outnumbers adult emergence (3).

From the statistical point of view, progeny production data deviated slightly from normality but remained symmetrical. However, it was decided not to apply classic parametric tests for comparisons between means. Nonparametric tests were not applicable either because of the extremely high number of ties. Nevertheless, visual comparisons of means and standard deviations of columns 1 and 2 of Table 1 suggest that late mortality is negligible, and that the constancy of adult emergence per host egg must be the result of mortality in the very first instar larvae, if a larval competition process is taking place.

SIMPLE CORRELATION ANALYSIS OF PARASITE SIZE VERSUS HOST EGG VOLUME AND PROGENY PRODUCTION PER HOST EGG: Average length of parasites (total or emerged, males or females) was correlated with progeny production per host egg, and the results showed that: a) as expected, correlation coefficients were positive between parasite size and host egg volume, and negative between parasite size and progeny production per host egg; b) in all cases correlation coefficients show a higher value between parasite size and progeny production per host egg than between parasite size and host egg volume; c) correlation coefficients *(r)* show higher statistical significance (measured by means of *t* values) when parasite size is correlated with total production per host egg than when it is correlated with other measurements of progeny production per host egg; d) all correlations are statistically significant in spite of very low *r* values between parasite size and host egg volume. Average length of emerged females and males as a function of total production per host egg is shown in Figs. 1 and 2, and their correlation coefficients indicated.

MULTIPLE CORRELATION ANALYSIS OF PARASITE SIZE VERSUS HOST EGG VOLUME AND PROGENY PRODUCTION PER HOST EGG: The fact that all simple correlation coefficients proved to be statistically significant justified a multiple correlation and regression analysis between these three variables. Conclusions are similar to the ones obtained from the simple correlation analysis, in the sense that: a) the regression coefficient of the effect of host egg volume is positive, while that of progeny production per host egg is negative; b) all multiple correlation coefficient *(R)* values show an extremely high statistical significance; c) the most significant *R* values are the ones correlating parasite size, host egg volume and total production per host egg ($R = 0.845$).

The coefficients representing the value that host egg volume and progeny production per host egg have in the regression equation show that the latter is greater (1.25 to 5.0 times) than the former. An evaluation of the degree in which each variable decreases the total sum of squares of parasite size (14) shows that the additional reduction of the total sum of squares of parasite size, due to total progeny production per host egg, is approximately 12-fold that due to host egg volume.

VITAL SPACE PER PARASITE: Having established that both host egg volume and progeny production per host egg have a statistically significant effect upon parasite size, it was of interest to express this relationship in a combined way. This is a logical step since positive and negative correlations between parasite size and host egg volume, and between parasite size and progeny production per host egg, respectively, make it obvious that they are the expression of the same process: competition for food.

Thus, Table 3 shows the relationship between parasite size and availability of host egg volume per individual, grouping all cases of parasites of the same average length, and averaging the host egg volume and the total progeny production per host egg. For example, line 3 shows there were 29 host eggs that produced emerged-adults of an average length of 1.00 mm, that the average volume of these eggs was 2.381 mm³, and that the average number of individuals produced per host egg was 7.83; thus, the average egg volume (in mm³) available to each parasite (here called vital space, as shown in column 5) is 0.3041 mm³, formed by the ratio of columns 3 and 4.

TABLE 3

Calculation of vital space and its relation to parasite length

Nº of host eggs	Average length of emerged adults (mm)	Average host egg volume (mm³)	Average total production per host egg (Nº ind.)	Vital space (mm³/parasite)
2	1.02	2.530	7.50	.3373
11	1.01	2.534	7.55	.3118
29	1.00	2.381	7.83	.3041
31	.99	2.351	7.90	.2976
20	.98	2.271	8.00	.2839
6	.97	2.284	8.50	.2687
8	.96	2.180	9.00	.2422
4	.95	2.168	9.00	.2409
2	.93	2.175	10.50	.2071
2	.91	2.160	13.00	.1662
2	.87	2.130	13.00	.1638

Fig. 3 shows the parasite length corresponding to a given value of host egg volume, with the regression line and correlation coefficient. The parameters of the regression line have a clear biological meaning: a is the minimum *theoretical* parasite length (0.77 mm in this case), and b the rate at which the parasites are capable of increasing in size with more vital space available to them.

A way of evaluating the effect of host egg volume availability on parasite size is by means of the concept of elasticity of a function, a concept commonly used in economics but rarely applied in ecology (4). The elasticity of a function

$$E_x(y) = \frac{dy/y}{dx/x}$$

and can be interpreted as an intrinsic rate of change, i.e., an instantaneous change by the unit of the dependent variable for a given change in the unit of the independent variable. Applying this definition to the function represented by the linear equation given in Fig. 3 we obtain

$$E_x(y) = \frac{bx}{a + bx}$$

where x is vital space and y parasite size, indicating that with increasing values of the former there is always a higher percentile increase of the latter.

DISCUSSION

Two important aspects of the developmental process in *Telenomus fariai* show interesting results from the ecological point of view. On the one hand there is a remarkable constancy of emerged adults per host egg. It is not known how much of this constancy is provided for by females laying a certain number of eggs proportional to the host egg volume, as suggested by LIMA (6), or by a very efficient larval competition process. The number of eggs laid by female parasites was not investigated in this experiment, but is is the belief of the author, that even if the female is capable of detecting the size of the host egg and laying a number of eggs proportional to it, the larval competition process plays a key role in determining the number of emerged parasites per host egg (13). The results of the present study suggest that any population regulation mechanism based on larval competition would operate during the youngest instars of the larval stage.

On the other hand, multiple correlation analyses clearly prove that both host egg volume *and* number of parasites produced per host egg are relevant factors in determining parasite size, although the latter is on the average three times as important as the former.

From the population of 117 host eggs analyzed, the average vital space was 0.2856 mm^3/parasite (SD= ± 0.0332) which corresponds to an average length of emerged adults of 0.984 mm (SD= ± 0.025). These results do not coincide with those reported by ZELEDÓN (15) who obtained a vital space of 0.178 mm^3/individual and an average parasite length of 0.996 mm (calculated from the author's original data). These differences could be due to one or more of the following factors: a) parasite populations were from a different origin (in Zeledón's experiments the parasites were from El Salvador); b) host species may be different subspecies, Zeledón does not indicate subspecies but this possibility is supported by the fact that eggs have different average volume values (2.022 and 2.134 mm^3 for Zeledón's and my experiments, respectively); c) Zeledón's calculation of vital space was based on emerged adults only, while mine was based upon total number of individuals produced (emerged adults + dead adults + dead pupae + dead larvae). However, similarity of vital space results can be shown by recalculating vital space for emerged adults only, and for the particular case of 12 adults emerging per host egg (close to the 11.34 average given by Zeledón); the result is a vital space of 0.180 mm^3/parasite, very close to Zeledón's figure of 0.178 mm^3/parasite.

SUMMARY

Some ecological aspects of the developmental process of the endophagous egg parasite *Telenomus fariai* when reared in *Triatoma phyllosoma pallidipennis* eggs, have been investigated. It was shown that mortality among pupae and last instar larvae does not account for the constancy in parasite progeny emergence per host egg, suggesting that if there is any population regulation mechanism based on larval competition, it would be operating among the youngest instars. Simple and multiple linear correlations between parasite size and host egg volume, and progeny production per host egg show that both factors are relevant in determing parasite size, but the effect of progeny production per host egg is on the average three times as important as host egg volume. Vital space (mm^3 of host egg volume available per parasite) shows an extremely high correlation (0.970) with parasite size. The elasticity function of vital space on parasite size shows that with increasing values of the former, there is always a higher percentile increase of the latter.

RESUMEN

En un estudio sobre algunos aspectos ecológicos del proceso de desarrollo del parásito endófago *Telenomus fariai* en uno de sus huéspedes, *Triatoma phyllosoma pallidipennis,* se concluye que la mortalidad pupal y de los últimos estadios larvales no explica la gran constancia de la emergencia de progenie por huevo del huésped. Esto sugiere que, de operar un mecanismo de regulación en la población, basado en la competencia larval, éste tendría lugar durante los estadios larvales más jóvenes. Las correlaciones lineales, simples y múltiples, entre el tamaño de los parásitos y el volumen del huevo del huésped, y la producción total de progenie por huevo del huésped, muestran que ambos factores influyen en determinar el tamaño de los parásitos; sin embargo, el efecto de la cantidad de progenie producida por huevo del huésped es, en promedio, tres veces más importante que el del volumen del huevo del huésped. El espacio vital (mm^3 de volumen del huevo del huésped disponible por individuo) muestra una correlación sumamente alta (0.970) con el tamaño de los parásitos. Se calculó la función de elasticidad del espacio vital sobre el tamaño de los parásitos, demostrándose que con disponibilidades crecientes de espacio vital hay siempre un aumento porcentual mayor en el tamaño de los parásitos.

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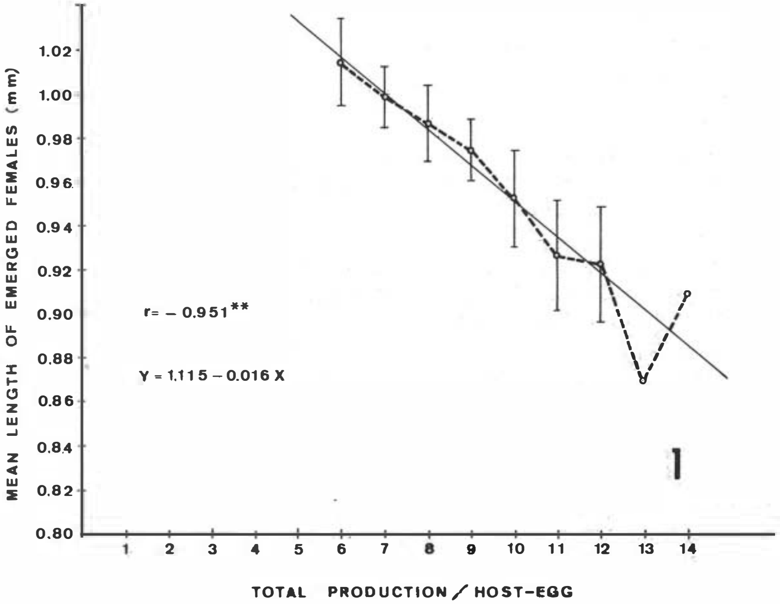
Fig. 1. Average length of emerged females per host egg as a function of total production per host egg. Broken line connects mean values; thin line is the regression line; vertical lines are one standard deviation about the mean (for x= 13, SD= O, and for x= 14 there is only one observation).

Fig. 2. Average length of total males per host egg as a function of total production per host egg. Lines as in Fig. 1.


MEAN LENGTH OF EMERGED FEMALES (mm)
1.02
1.00
0.98
0.96
0.94
0.92
0.90
0.88
0.86
0.84
0.82
0.80
r= – 0.951**
Y = 1.115 – 0.016 X
1
1 2 3 4 5 6 7 8 9 10 11 12 13 14
TOTAL PRODUCTION / HOST-EGG

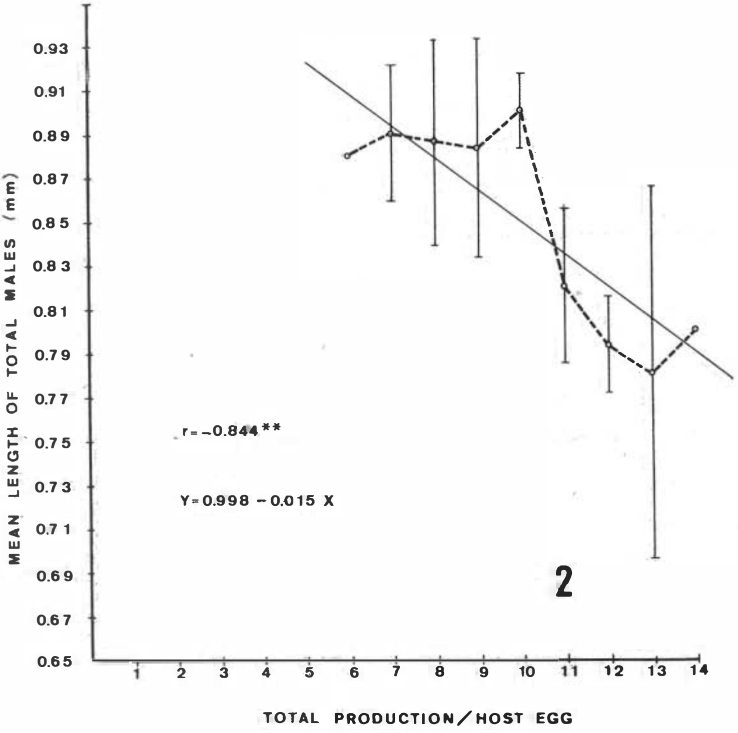

MEAN LENGTH OF TOTAL MALES (mm)
0.93
0.91
0.89
0.87
0.85
0.83
0.81
0.79
0.77
0.75
0.73
0.71
0.69
0.67
0.65
r= –0.844**
Y= 0.998 – 0.015 X
2
1 2 3 4 5 6 7 8 9 10 11 12 13 14
TOTAL PRODUCTION / HOST EGG

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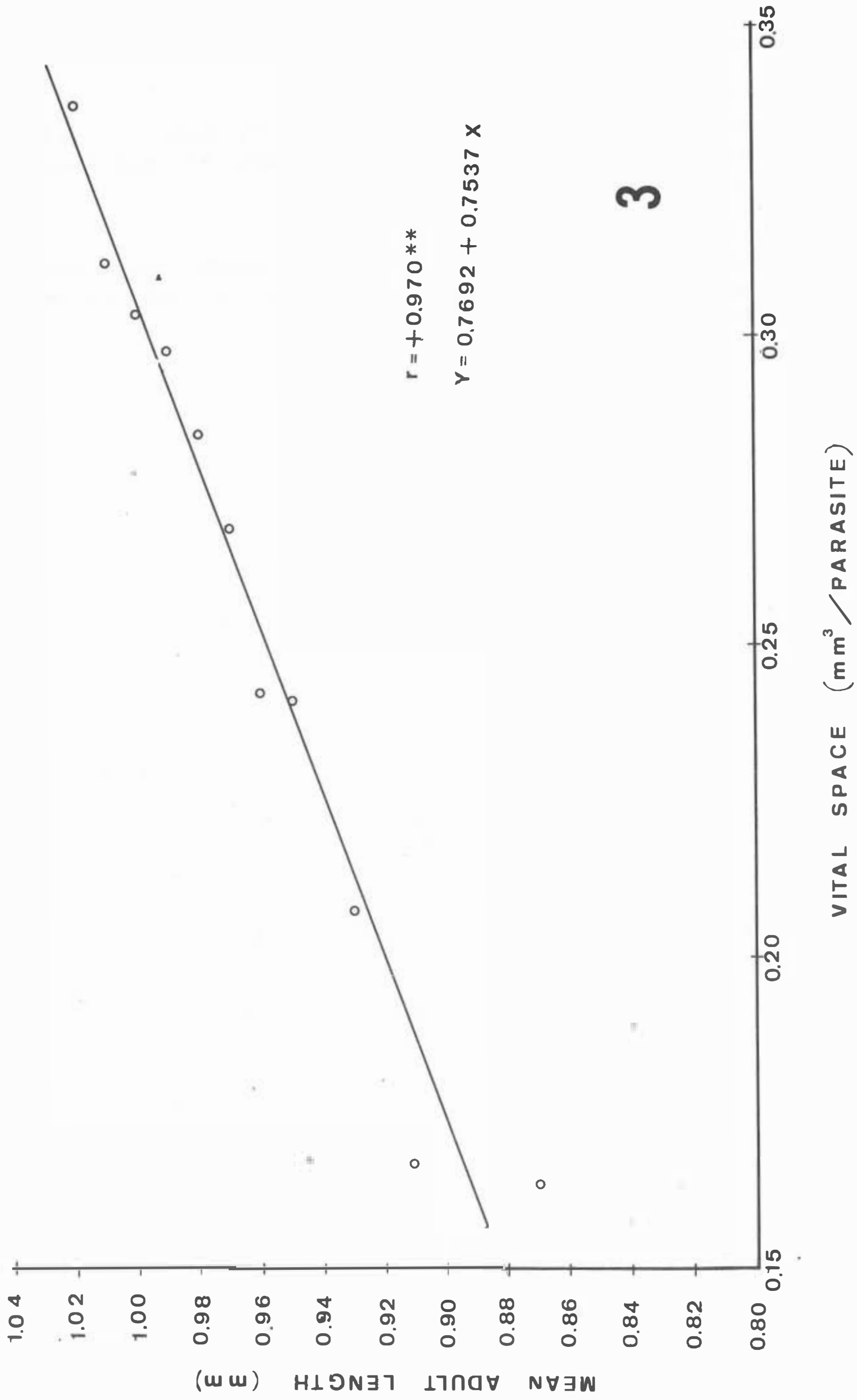
Fig. 3. **Parasite size as a function of vital space.**


r = +0.970**
Y = 0.7692 + 0.7537 X
3
VITAL SPACE (mm³/PARASITE)
MEAN ADULT LENGTH (mm)
0.15
0.20
0.25
0.30
0.35
0.80
0.82
0.84
0.86
0.88
0.90
0.92
0.94
0.96
0.98
1.00
1.02
1.04

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