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THE IMPACT OF VARIOUS ENVIRONMENTAL FACTORS
ON Trichogramma pretiosum Riley BIOLOGY
WHEN REARED ON SOUTHWESTERN CORN BORER EGGS

by

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B.S., Iowa State University, 1978

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

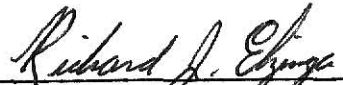
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INTRODUCTION

Trichogramma pretiosum Riley is one of a complex of Trichogramma spp. (T. minutum and T. exiguum) known to attack southwestern corn borer, Diatraea grandiosella (Dyar), (SWCB) eggs in Kansas. Species of Trichogramma have been reported to parasitize SWCB eggs across the SWCB's geographic range (Davis, 1933; Walton and Bieberdorf, 1948; Rolston, 1955; and Henderson and Davis, 1969). No other parasites are known to significantly impact SWCB populations in Kansas. Wilbur et al. (1950) unsuccessfully attempted to establish Apanteles diatreae Muesbeck and Macrocentrus gifuensis Ashmead in Kansas as biological control agents of the SWCB.

Economic corn yield losses are caused by second generation SWCB populations. The late second and partial third generation SWCB egg populations have been significantly reduced by Trichogramma parasitism (personal observation). However, this portion of the SWCB population has little effect on corn yield reduction. Yield loss due to SWCB tunneling decreases as the corn plant nears physiological maturity (Whitworth, 1980). During most years, late second and third generation SWCB larvae do not initiate stalk tunneling until after physiological maturity of the corn plant. Based on SWCB oviposition patterns the majority of second generation eggs escape parasitism, which can result in an economic yield loss.

High levels of parasitism during late second and third generations and the density-dependent relationship between Trichogramma and SWCB eggs indicate that Trichogramma may have the potential to effectively reduce damaging second generation SWCB populations. Augmentation of Trichogramma populations during the SWCB oviposition period could synchronize the two populations and increase the potential of Trichogramma. The objectives of this study were to: (1) determine the effect of several environmental conditions on T. pretiosum developmental time, fecundity, longevity, and sex ratio; (2) survey second generation SWCB oviposition and parasitism rates; and (3) develop a theoretical model to investigate the potential of T. pretiosum as a biological control agent of the SWCB.

METHODS AND MATERIALS

Trichogramma were field collected on 29 July 1980 and 1 August 1980 in Riley and Stafford counties, Kansas, respectively, and reared in the laboratory utilizing southwestern corn borer eggs as hosts, at 26.5°C with 16 h photophase (supplied from auxiliary lighting) and 40 \pm 4% RH. Dr. E.R. Oatman identified the specimens as T. pretiosum Riley. Adult wasps were allowed to oviposit in host eggs without feeding. Host material was reared according to Davis (1976).

Effect of Constant Temperature

A completely randomized design was used with two replications of six treatments. Temperatures (17°C, 20°C, 22°C, 25°C, 30°C, and 35°C) constituted treatments. Photophase (14 h) and humidity (60% RH) were held constant for all treatments. Petri-dishes (8.74 x 1.91 cm) served as arenas for parasitism of fresh (less than 24 hours old) SWCB eggs. Duration of T. minutum development reported by Lund (1934) was used to determine the number of dishes per treatment. Circular styrofoam pads 0.64 cm thick divided into four equal quadrants were cut to fit snugly into each container. Forty (10 per quadrant) wax paper discs each containing a single SWCB egg were stapled to the styrofoam before insertion into the petri-dishes. The styrofoam pads were then placed firmly in the petri-dishes and rubber tubes (1.27 x 2.54 cm) were inserted into a 1.27 cm hole at the bottom-center of each dish. To prevent parasite escape, the tops were sealed with Handi-Wrap®.

Twenty newly emerged mated female wasps were aspirated into a glass vial (one per petri-dish) that was closed on the distal end with muslin using two sections of rubber tubing (0.63 cm ID). Cotton plugs were inserted into the proximal end of the vials after collection. Wasps were then released into each dish by inserting a glass vial into the rubber tube at the petri-dish center, and the dishes were set on 28 gram (1 oz.) plastic cup stands. Two hours after release, the Handi-Wrap[®] covers and wasps were removed from the dishes, and the dishes containing parasitized host eggs were placed in a programmable growth chamber.

Initial observations were made 24 hours after removal of the female wasps. Subsequent observations were made at 12 hour intervals until completion of parasite development. Two quadrants (20 host eggs) from a randomly selected petri-dish were examined for parasites during each observation period. The number of Trichogramma individuals per observation period was uncontrollable, due to differences in the number of eggs deposited. A destructive sampling procedure was used as SWCB eggs were dissected to identify parasite egg, larval, prepupal, and pupal growth stages. Adult emergence was recorded. Trichogramma stages were determined using Flanders' (1937) description. A dissecting microscope with an 8X ocular and 4X lens was used in determining the parasite stage and to measure parasite and host size. Date, observation period, and number of parasites per host egg were recorded. The number of adult parasites per host egg was determined by placing individual host eggs from two quadrants per replication in 28 gram plastic cups and counting the number of emerging wasps. Upon emergence, adults were transferred individually into 28 gram

cups and supplied SWCB eggs for oviposition. Fecundity was determined by counting the number of eggs oviposited in SWCB eggs plus dissecting dead females on microscope slides to determine the number of retained eggs.

The observed percent life stage completion data for each temperature was fit using probit analysis. Cumulative percent stage completion constituted the dependent variable and days after oviposition, the independent variable. Fifty percent stage completion and the variance about the fifty percent point were determined. Median or 50th percentile duration of each life stage represented the time between 50th percentile stage completion of successive stages.

Effect of Fluctuating Temperature

Similar procedures were followed to ascertain the effect of fluctuating temperature on Trichogramma developmental rate, longevity, fecundity, and sex ratio. A completely randomized design was again used with two replications of four treatments. Fluctuating regimes (30°C , 28°C - 32°C , 26°C - 34°C , and 22°C - 38°C constituted treatments. Temperatures fluctuated around a 30°C mean every 24 hours (Appendix V). The photophase was 14 hours and the relative humidity, $60 \pm 10\%$.

Effect of Humidity

The procedures described for constant temperatures were also used to study humidity effects. Photophase (14 h) and temperature (30°C) were held constant across treatments. A completely randomized design was used with two replications of three treatments: $20 \pm 10\%$ RH, $60 \pm 10\%$ RH, and $80 \pm 10\%$ RH. Humidities were maintained using a Bio-Temp Weathersetter[®] programmable growth chamber manufactured by Scientific, Inc.

Effect of Photophase

Photophase effects were studied using the procedures described for constant temperatures. Humidity was held at $60 \pm 10\%$ RH and temperature was held at 30°C across treatments. A completely randomized design was used, two replications of three treatments. Photophases (16 h, 14 h, and 12 h) constituted treatments.

Seasonal Occurrence

Seasonal oviposition by southwestern corn borer and parasitism by Trichogramma were observed in the field during 1978 and 1979. Sampling began 20 July 1978 and 19 July 1979 at Sandyland Experiment Field, St. John, Kansas. A sample universe was defined as $121.9 \times 30.5 \text{ m}$ (3715.5 m^2). A stratified random sampling method was used with two samples selected randomly from each of 40 strata (1 corn row = 1 stratum). Sample units (corn plants) were marked with blue survey flags in order to relocate plants during sampling.

Corn plants were examined at two day intervals in 1978 and three to four day intervals (1978 results indicated that three to four day samples were sufficient) in 1979. The entire corn plant (leaves, stem, and ears) was examined for freshly oviposited and parasitized SWCB eggs. Newly oviposited SWCB eggs were circled with indelible ink. The date SWCB oviposition or parasitism occurred and number of SWCB eggs per mass were recorded. During 1979, SWCB egg mass height (leaf node above ground level) on the corn plant was recorded (Appendix VII).

To determine if artificial and natural SWCB infestations were subject to similar seasonal parasitism, laboratory egg masses were

periodically (11, 14, and 17 August 1979) placed in the field near SWCB eggs. Artificially infested egg masses were placed at heights corresponding to natural egg masses on the corn plants. Parasitized egg masses (natural and artificial) were taken to the laboratory and parasites allowed to emerge. The number of parasites per host egg and sex ratio were recorded.

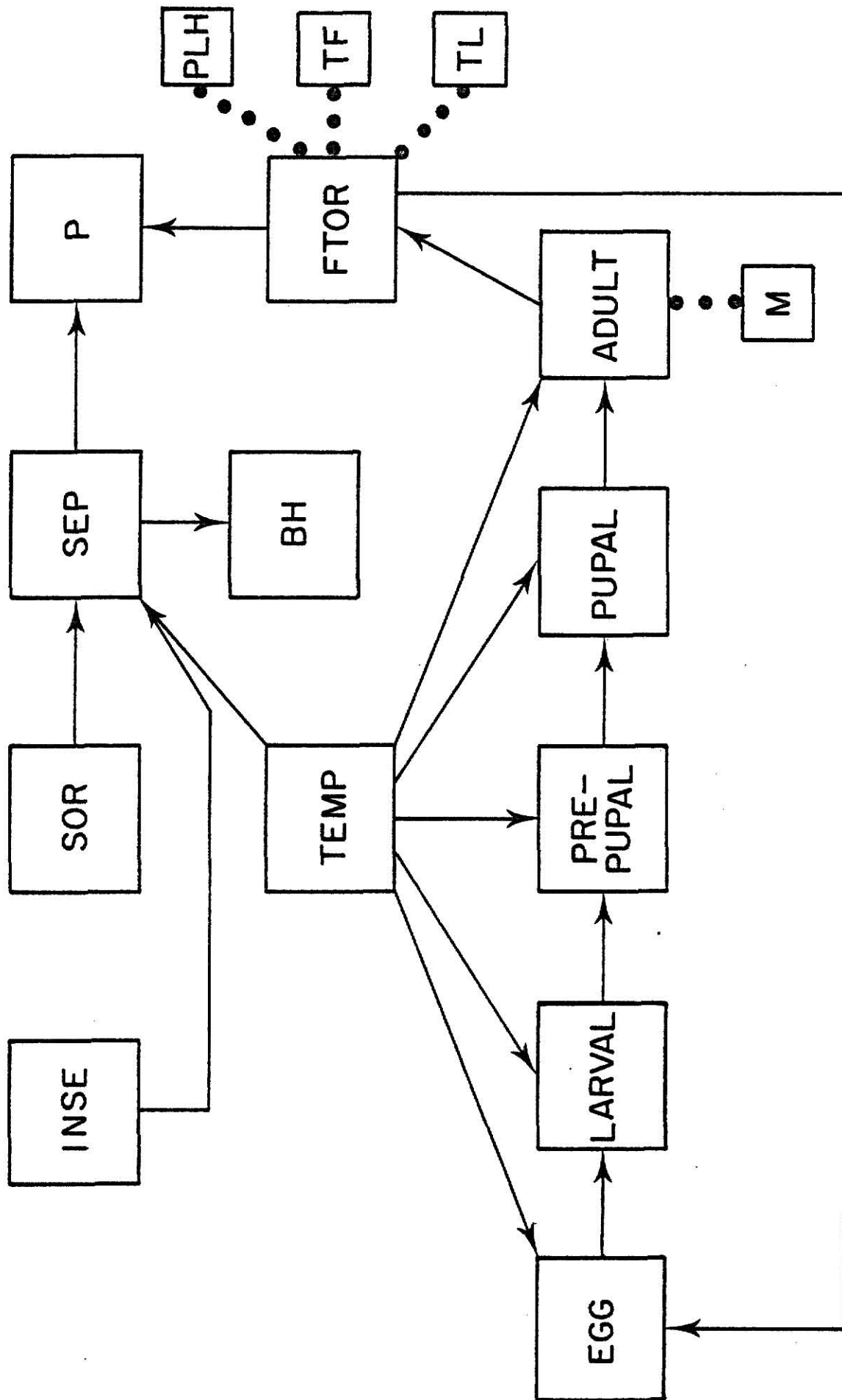
Theoretical Model

A theoretical model was developed using results from the previous studies to explore the impact of T. pretiosum on SWCB egg populations. Using the model, several questions were investigated: (1) how many T. pretiosum generations can be completed during the second generation SWCB oviposition period; (2) what is the length of a T. pretiosum generation under a defined set of conditions; (3) can naturally occurring T. pretiosum populations effectively reduce SWCB egg populations; and (4) would augmentation increase T. pretiosum's effectiveness.

To investigate the potential of Trichogramma, a hypothetical system was defined as a one acre corn field in south central Kansas with a plant population of 24,000 plants per acre. No parasites, predators, or pathogens other than T. pretiosum interacted with the SWCB egg population. Model simulations were limited to the second generation SWCB oviposition period (26 July 1979-22 August 1979).

A block diagram of the T. pretiosum life system is shown in Figure 1. Blocks represent system components, and each arrow indicates the existence of a cause and effect relationship. Dotted lines indicate system parameters. T. pretiosum life stages (egg, larval,

Figure 1. Block diagram of the T. pretiosum life system. Blocks represent system components, and each arrow indicates the existence of a cause and effect relationship. Dotted lines indicate system parameters.



prepupal, and pupal) were modeled and moved through time using developmental time equations and a time-varying distributed delay. K values were determined for egg, larval, prepupal, and pupal T. pretiosum life stages and the SWCB egg stage using the equation: $K = \bar{x}^2/s^2$, where \bar{x} is the estimated population mean and s^2 is the estimated population variance (Welch et al., 1978). K values and a complete model description are shown in Appendix I. Because adult wasp longevity was short (approximately two days under July and August temperatures) with little variation, a discrete delay with 48 one-hour steps was used.

SWCB eggs were progressed through time using thermal-unit accumulation. A time-varying distributed delay with a K value of 24 was used. The SWCB egg population (SEP) was calculated by multiplying the initial number of SWCB eggs (INSE) to be deposited over the season times the SWCB oviposition rate (SOR). When eggs reached the blackhead (BH) stage they were removed from the population as laboratory studies indicated that blackhead SWCB eggs are not readily attacked by T. pretiosum females (unpublished data, Calvin). This happened after 85 thermal units accumulated, as established by an Insect Ecology laboratory exercise.

The daily oviposition rate of T. pretiosum was described by the equation: $FTOR = ADULT \times (TF/TL) \times PLH$, where FTOR is the female Trichogramma oviposition rate, ADULT is the adult female T. pretiosum population, TF is female T. pretiosum fecundity, TL is female T. pretiosum longevity, and PLH is the probability of locating a host. Assuming that a wasp oviposits three ova/host egg, daily parasitism (P) was 1/3 of the daily T. pretiosum ovipositional rate.

Data were available for all variables and parameters except the initial adult female T. pretiosum population (ADULT), the number of second generation SWCB eggs oviposited (INSE), probability of locating a host (PLH), and immature T. pretiosum mortality (M). Because data were unavailable, levels of each variable and parameter were set within ranges thought to occur under natural conditions. Levels were reinitialized for each computer run. Levels of the two unknown system variables were: (1) initial adult T. pretiosum female population--50, 100, 500, 1000 adult females/acre; (2) total seasonal SWCB egg population--48,000, 96,000, 192,000 eggs/acre. Levels of the unknown system parameters were: (1) probability of locating a host--25%, 50%, 75%; (2) T. pretiosum immature mortality--25%, 50%, 75%. All possible combinations of the variables and parameters were run and percent SWCB egg parasitism was predicted. T. pretiosum age distribution, generation time, and number of generations during the second generation SWCB oviposition period were determined for selected model runs.

Two augmentation programs were compared to no augmentation. Program one consisted of introducing 500, 1000, or 2000 additional female wasps seven days after model initiation. The second program involved two releases of 500, 1000, or 2000 female wasps; the first release four days and the second release eight days after the simulation began.

Augmentation programs were selected based on T. pretiosum generation time in relation to the SWCB oviposition period. Wasp populations were released to fill in between natural population generations and increase the period of parasitism during second generation SWCB oviposition. Under both schemes, releases were made before peak SWCB oviposition with the

assumption that later generations of the released wasps would parasitize SWCB eggs laid after peak oviposition.

More than two releases were not considered because of increased energy and labor costs and the grower's small profit margin. One and two releases were used because this corresponds to the present number of chemical applications used to control SWCB populations.

RESULTS AND DISCUSSION

Effect of Constant Temperature

The median durations and standard errors of the egg, larval, prepupal, and pupal stages and developmental time from oviposition to 50% completion of adult emergence are presented in Table 1. Sample size affected the accuracy of the median stage duration estimates and was exhibited in the standard error. Large fluctuations in percentage stage completion were the result of small sample sizes and destructive sampling (Appendix II).

Median developmental times for T. pretiosum life stages are plotted in Figures 2 through 6. Curve equations and 95% confidence intervals (broken lines) about the curves are included. Vertical bars represent 95% confidence intervals about the observed 50% stage completion. A second degree polynomial was used to describe the relationship of developmental time and temperature for each life stage. Optimum development was predicted to be 30°C for all life stages. However, the actual optimal developmental time probably falls somewhere between 25°C and 35°C.

Because an accurate estimate of the minimum threshold temperature is essential, many methods have been proposed to fit the developmental time curve. Logan (1977) criticized the use of least square polynomials to describe temperature-dependent life history parameters. However, this study is only concerned with the temperature range encountered

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Table 1. Median or 50th percentile durations and standard errors (Days)^a of T. pretiosum

Riley life stages at constant temperatures.

Temperature (C°)	Egg	Larval	Prepupal	Pupal	Oviposition- Adult
17	3.27 ± 0.14	4.08 ± 0.61	10.08 ± 0.98	11.00 ± 1.01	28.43 ± 0.56
20	2.20 ± 0.49	2.87 ± 0.70	4.75 ± 1.53	7.59 ± 1.96	17.41 ± 1.85
22	2.69 ± 0.17	1.92 ± 0.51	4.03 ± 0.27	7.44 ± 0.36	16.08 ± 0.31
25	1.15 ± 0.16	1.95 ± 0.17	3.10 ± 0.29	3.80 ± 0.12	9.79 ± 0.12
30	0.91 ± 0.06	1.32 ± 0.37	2.70 ± 0.21	2.87 ± 0.34	7.80 ± 0.23
35	1.30 ± 0.37	1.52 ± 0.50	3.32 ± 0.48	4.04 ± 0.34	10.18 ± 0.31

^a50% of the population completed the stage in this time period.

Figure 2. Median developmental time (in days) for the egg stage of T. pretiosum at constant temperatures.

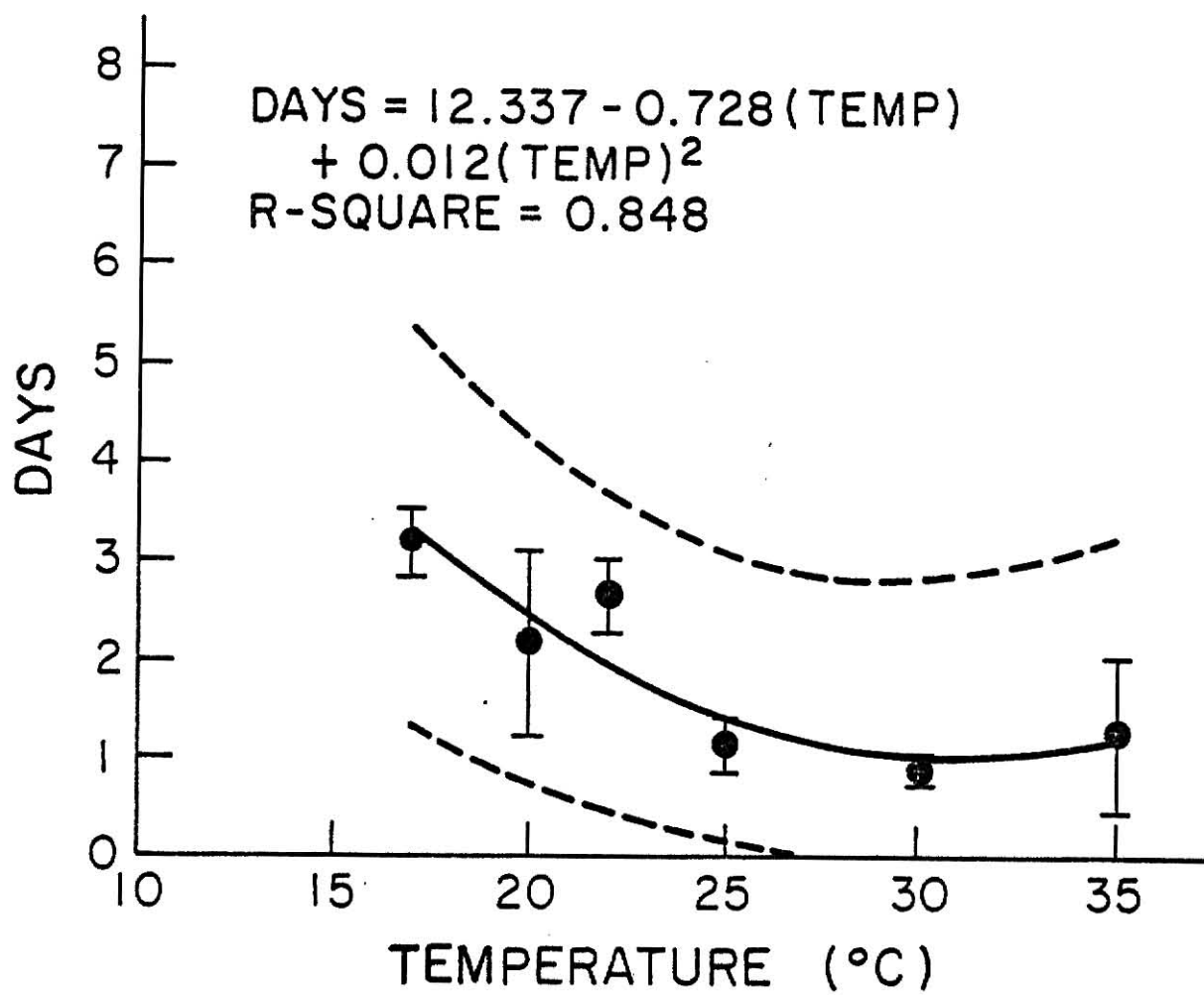


Figure 3. Median developmental time (in days) for the larval stage of T. pretiosum at constant temperatures.

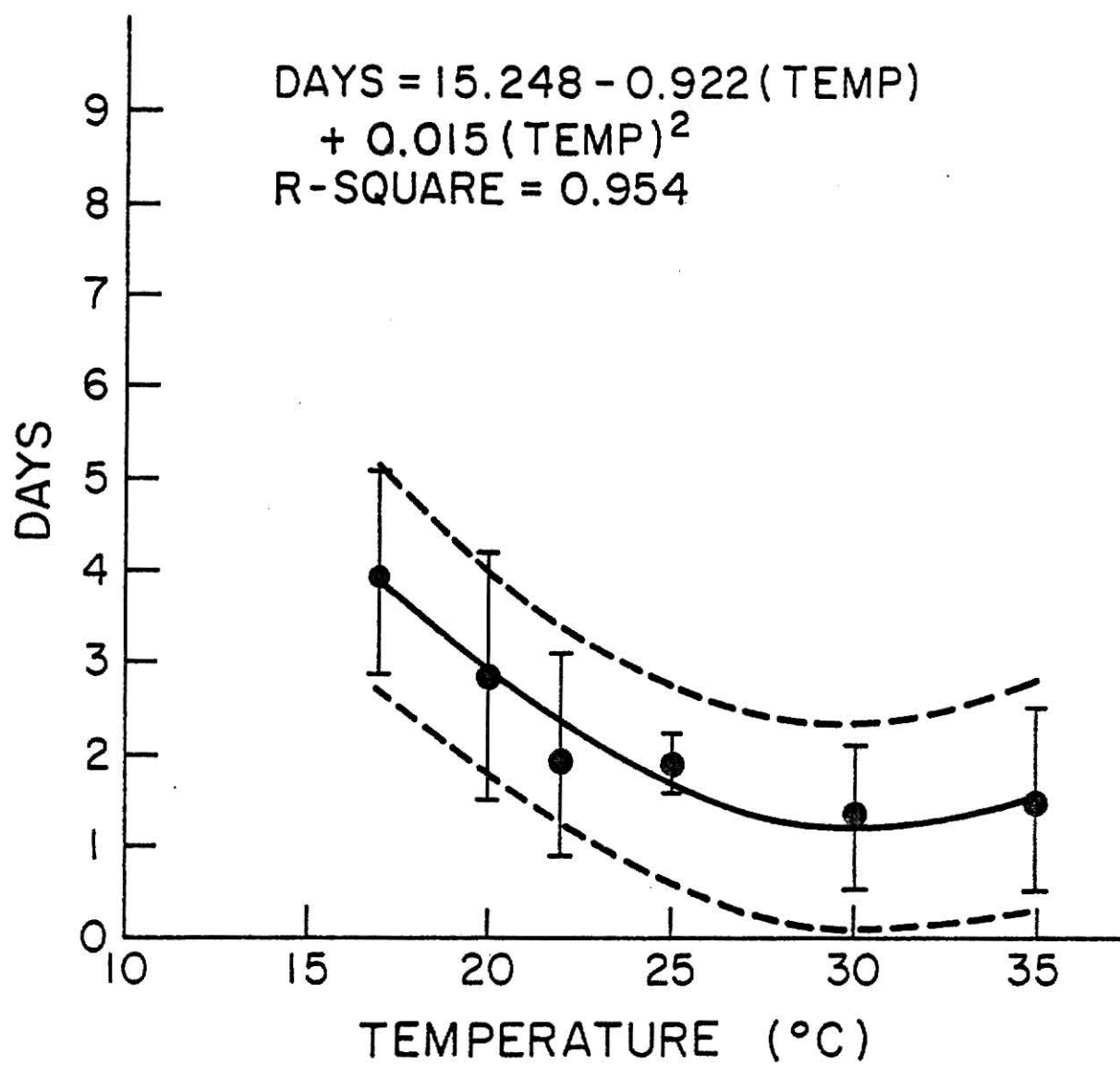


Figure 4. Median developmental time (in days) for the prepupal stage of T. pretiosum at constant temperatures.

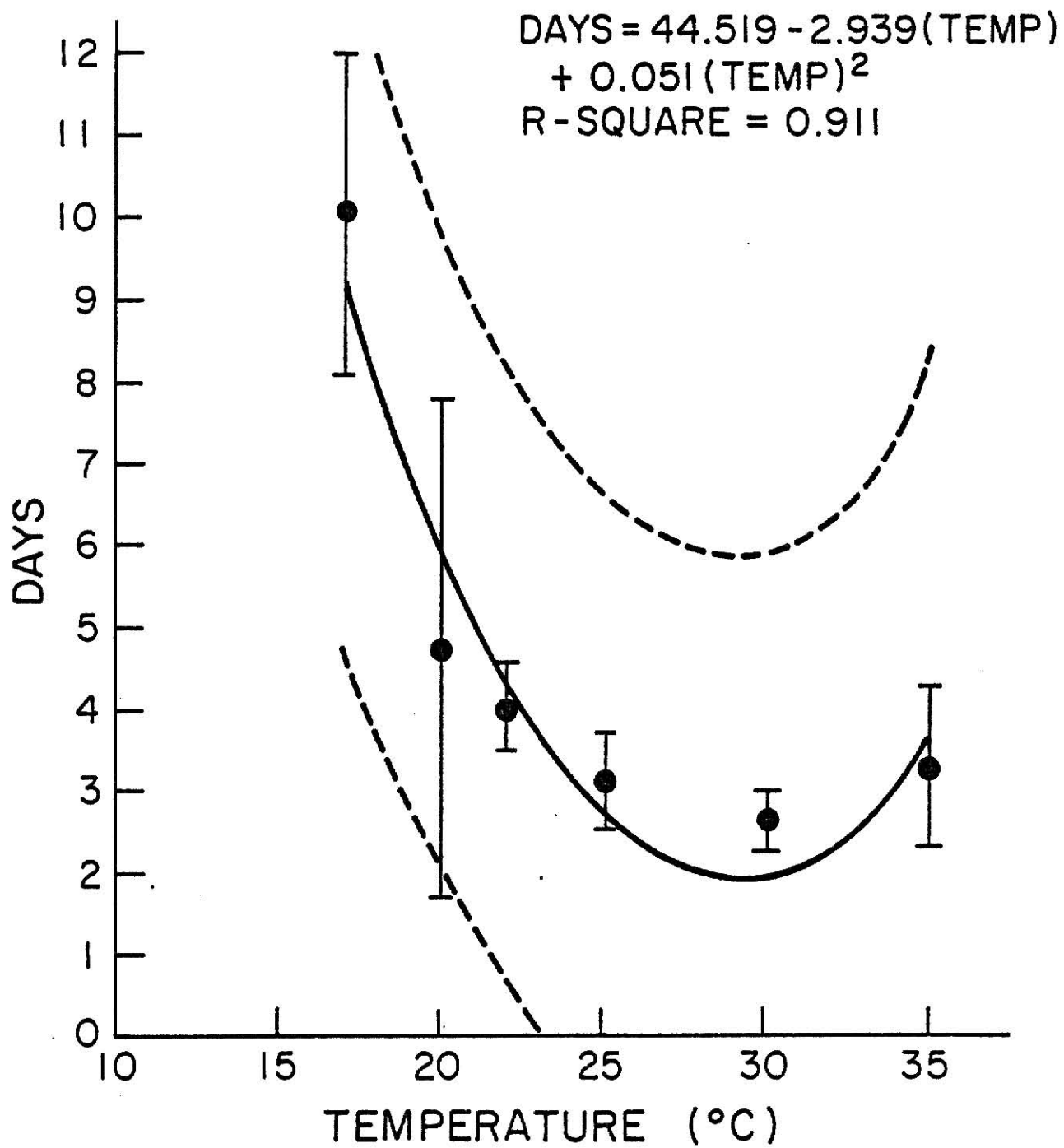


Figure 5. Median developmental time (in days) for the pupal stage of T. pretiosum at constant temperatures.

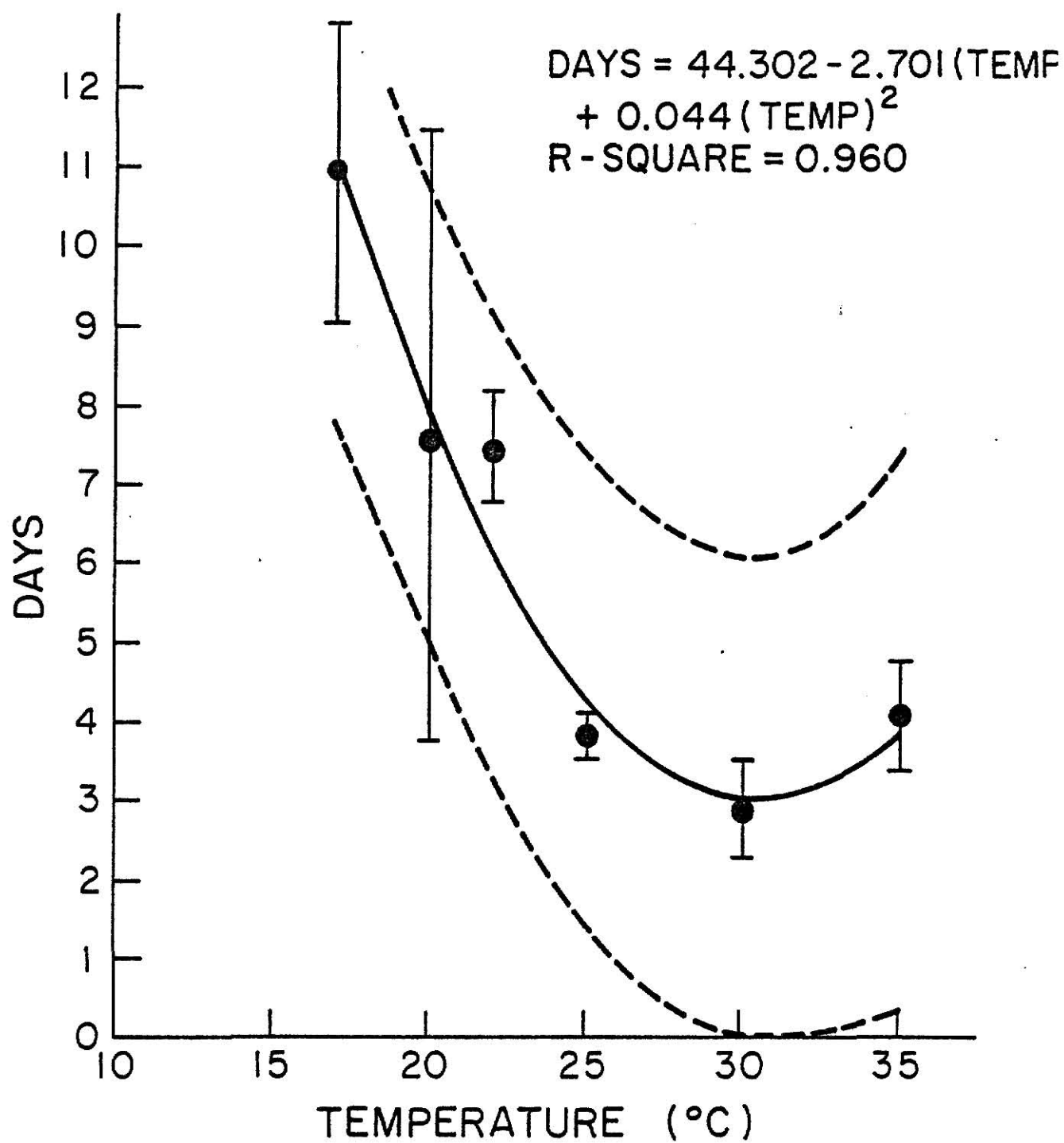
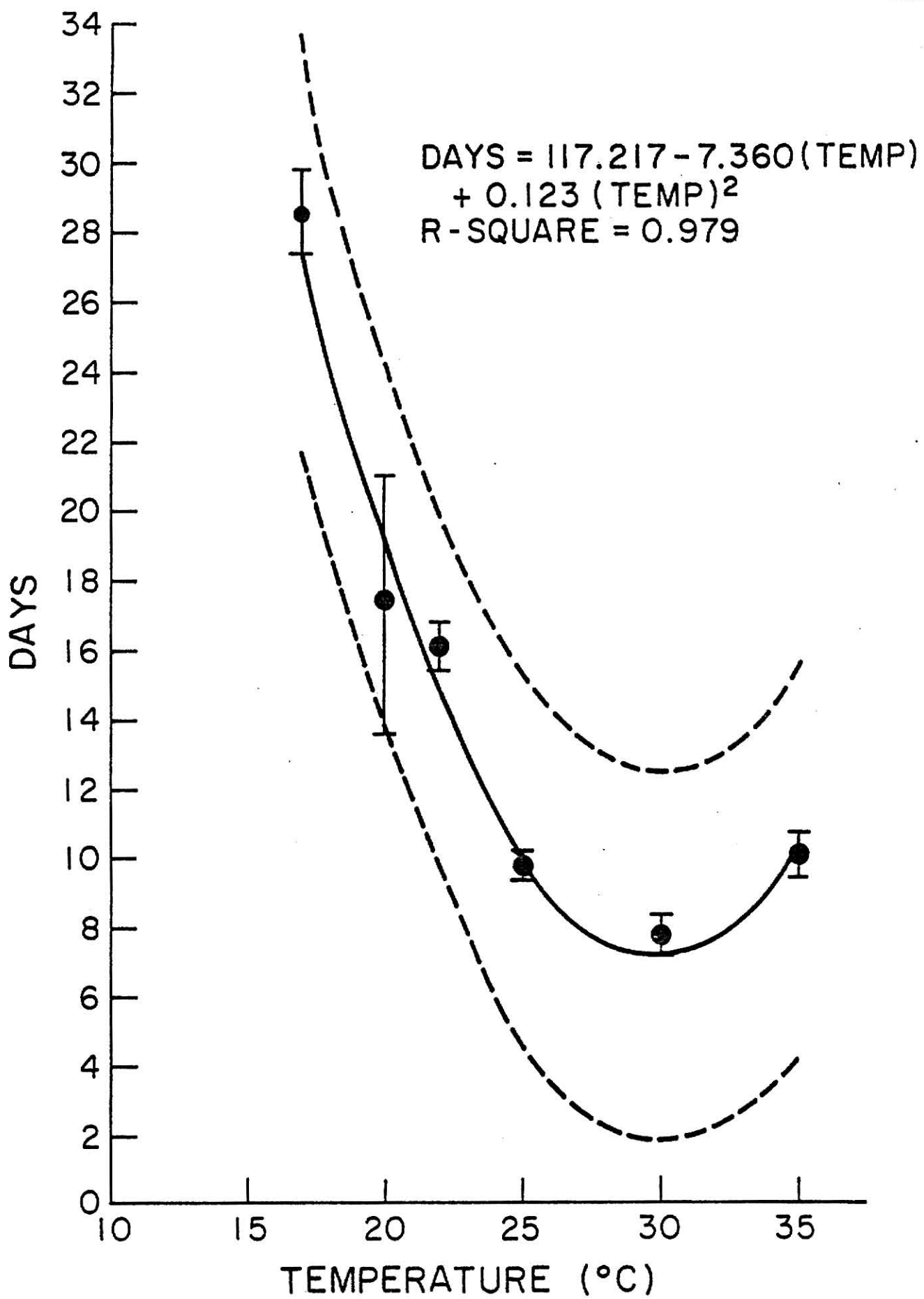


Figure 6. Median developmental time (in days) from oviposition to adult emergence at constant temperatures.



by T. pretiosum during second generation SWCB oviposition (July and August. Extreme average daily temperatures (above 35°C or below 22°C) are uncommon during this time.

Number of parasites per host egg and host size have been shown to influence Trichogramma spp. developmental time (Barber, 1937; Marston and Ertle, 1973). The effect of host volume (HV) and parasites per host egg (PPH) was variable across temperatures (Appendix III). Variability in the effect of HV and PPH between temperatures was probably caused by sample size, experimental error, and/or a HV-PPH interaction. More research is needed to split out the main effects of HV and PPH on developmental time. Because of the small amount of variability in developmental times within a temperature, PPH and HV were considered to have a minor effect on developmental time. Neither PPH nor HV were taken into account when determining the developmental time curves.

T. pretiosum adult longevity at constant temperatures is presented in Table 2. Male, female, and average longevity were not significantly different ($P>0.05$) between 20°C and 30°C. Longevity was greatly increased at 17°C. Female and average fecundity significantly decreased at 35°C. Under cool temperatures, an insect's metabolism slows and activity and water loss decrease. T. pretiosum reared under low temperatures would use nutrient reserves at a lower rate and live longer (unless below the critical threshold). The converse would occur at high temperatures. Supplementing food greatly increases adult Trichogramma longevity (Ashley and Gonzalez, 1974). The lack of feeding in these laboratory

Table 2. T. pretiosum Riley longevity (days) after adult emergence when reared at constant temperatures.^a

Temperature (C°)	Male Longevity	Female Longevity	Average Longevity
17	7.33 a	7.67 a	7.50 a
20	1.50 b	2.19 b	2.00 b
22	1.83 b	1.89 b	1.87 b
25	1.42 b	1.95 b	1.75 b
30	1.30 b	1.83 b	1.72 b
35	0.80 b	0.60 c	0.73 c

^aNumbers followed by the same letter in the same column are not significantly different ($P>0.05$) using Duncan's New Multiple Range Test.

Table 3. T. pretiosum Riley female fecundity and sex ratio when reared at constant temperatures.^a

Temperature (C°)	Fecundity	Sex Ratio ^b
17	19.50 abc	.577
20	22.27 a	.720
22	13.00 bc	.537
25	19.54 ab	.647
30	9.85 c	.732
35	9.00 c	.538

^aNumbers followed by the same letter in the same column are not significantly different ($P>0.05$) using Duncan's New Multiple Range Test.

^bNumbers represent the female proportion of the population.

trials may, therefore, have an affect on the model's ability to predict field behavior of these populations.

The effect of temperature on fecundity and sex ratio was investigated (Table 3). Fecundity was not significantly ($P>0.05$) affected between 17°C and 25°C , with the exception of 22°C . Low fecundity at 22°C was probably caused by low sample size and chance, rather than any biological phenomenon. Lower fecundity at 30°C and 35°C was probably the result of less food reserves available for ova production. Sex ratio was believed to be affected by the number of parasites per host and not temperature (Appendix IV). Lund (1934) found no consistent relationship between temperature and sex ratio. Mortality may have contributed to sex ratio differences.

Effect of Fluctuating Temperature

Median durations and standard errors of egg, larval, prepupal, and pupal stages and developmental time from oviposition to 50% completion of adult emergence for fluctuating temperatures are presented in Table 4. At constant temperatures between 25°C and 35°C , developmental times were not considered different. Small differences in developmental time were expected for the 28°C - 32°C and 26°C - 34°C fluctuating regimes, as compared to the constant 30°C regime, since both fall within the 25°C - 35°C range. A longer developmental time was expected for the 22°C - 38°C regime. To determine why the actual developmental time was not greater, the developmental time curve of oviposition to 50% adult emergence (Figure 6) was used to predict developmental time under a 22°C - 38°C fluctuating regime. Developmental time was predicted by breaking

Table 4. Median or 50th percentile durations and standard errors (Days)^a of T. pretiosum

Riley life stages when reared under fluctuating temperature regimes.

Temperature (C°)	Egg	Larval	Prepupal	Pupal	Oviposition- Adult
30	0.91 \pm 0.06	1.32 \pm 0.37	2.70 \pm 0.21	2.87 \pm 0.34	7.80 \pm 0.23
28-32	1.24 \pm 0.04	1.05 \pm 0.40	2.68 \pm 0.47	2.94 \pm 0.32	7.91 \pm 0.15
26-34	1.15 \pm 0.11	1.04 \pm 0.11	2.82 \pm 0.09	2.66 \pm 0.19	7.67 \pm 0.06
22-38	1.35 \pm 0.18	1.30 \pm 0.19	3.14 \pm 0.56	3.88 \pm 0.63	9.67 \pm 0.26

^a50% of the population completed the stage in this time period.

Table 5. T. pretiosum Riley longevity (days) after adult emergence when reared under fluctuating temperature regimes.^a

Temperature (C°)	Male Longevity	Female Longevity	Average Longevity
30	1.30 a	1.83 a	1.72 ab
28-32	1.00 a	1.23 a	1.14 c
26-34	2.50 a	2.50 a	2.50 a
22-38	1.00 a	1.35 a	1.25 bc

^aNumbers followed by the same letter in the same column are not significantly different ($P>0.05$) using Duncan's New Multiple Range Test.

Table 6. T. pretiosum Riley female fecundity and sex ratio when reared under fluctuating temperature regimes.^a

Temperature (C°)	Fecundity	Sex Ratio ^b
30	9.85 a	.732
28-32	14.53 a	.571
26-34	15.71 a	.571
22-38	11.25 a	.619

^aNumbers followed by the same letter in the same column are not significantly different ($P>0.05$) using Duncan's New Multiple Range Test.

^bNumbers represent the female proportion of the population.

the fluctuating regime into segments of constant temperatures based on the programmable growth chamber's fluctuation regime (Appendix V). The predicted developmental time for 22°C-38°C was 9.25 days, compared to 9.67 days under actual conditions. Calculations are shown in Appendix VI.

The three fluctuating temperature regimes are close to the ranges occurring during July and August in central Kansas. Most average daily temperatures during July and August range from approximately 22°C-35°C. Although fluctuating temperatures may significantly affect developmental time at lower temperatures, fluctuation appears to have little affect on development at temperatures commonly occurring during second generation SWCB oviposition.

Adult male and female longevity were not significantly ($P>0.05$) affected by fluctuating temperatures (Table 5). However, when longevity was averaged, 26°C-34°C appeared to be significantly different ($P<0.05$). Based on the results, no explanation for the difference was attempted.

Fecundity was not significantly different ($P>0.05$) between fluctuation regimes (Table 6). Since developmental times were equal, energy spent during development would be approximately the same. Therefore, fecundity should be similar for each fluctuating regime. Sex ratio was influenced by the number of parasites per host egg.

Effect of Humidity

Increasing relative humidity caused an increase in developmental time (Table 7). Lund (1934) observed a similar trend in T. minutum

Table 7. Median or 50th percentile durations and standard errors (Days)^a of T. pretiosum Riley life stages when reared at three relative humidities.

Relative Humidity (%)	Egg	Larval	Prepupal	Pupal	Oviposition-Adult
80	1.29 ± 0.26	1.13 ± 0.19	2.18 ± 0.14	2.41 ± 0.22	7.01 ± 0.22
60	0.91 ± 0.06	1.32 ± 0.37	2.70 ± 0.21	2.87 ± 0.34	7.80 ± 0.23
20	1.70 ± 0.18	1.41 ± 0.27	3.31 ± 0.19	3.71 ± 0.14	10.13 ± 0.30

^a50% of the population completed the stage in this time period.

Table 8. T. pretiosum Riley longevity (days) after adult emergence when reared at three relative humidities.^a

Relative Humidity (%)	Male Longevity	Female Longevity	Average Longevity
80	1.00 a	1.45 a	1.21 a
60	1.30 a	1.83 a	1.72 a
20	2.25 a	3.80 b	3.11 b

^aNumbers followed by the same letter in the same column are not significantly different ($P>0.05$) using Duncan's New Multiple Range Test.

Table 9. T. pretiosum Riley female fecundity and sex ratio when reared at three relative humidities.^a

Relative Humidity (%)	Fecundity	Sex Ratio ^b
80	26.20 a	.480
60	9.85 b	.732
20	12.20 b	.455

^aNumbers followed by the same letter in the same column are not significantly different ($P>0.05$) using Duncan's New Multiple Range Test.

^bNumbers represent the female proportion of the population.

development. All life stages developed faster when the relative humidity was 80%, except the egg stage which was completed more rapidly at 60% RH. Developing T. pretiosum are protected from desiccation to some extent by the host egg chorion. However, water loss does occur at low relative humidities. Stress caused by water loss is believed to be responsible for increasing developmental time. Since water is essential for many metabolic processes, low water availability could slow growth and development of T. pretiosum.

An irrigated corn field in Kansas contains a variable microclimate. During July and August, relative humidities may be as low as 20%, but within the microhabitat next to a corn leaf, humidity is probably higher. Plant respiration keeps humidity high near the corn leaf surface. SWCB eggs parasitized by Trichogramma would probably not be exposed to a relative humidity as low as 20%.

Adult longevity significantly increased ($P < 0.05$) at 20% RH (Table 8). At low relative humidities, T. pretiosum may be less active in order to conserve water and energy. Laboratory T. pretiosum tended to be less active at low relative humidities.

Average female fecundity and sex ratio are presented in Table 9. Fecundity was highest at 80% RH. At 80% RH, water was not a limiting factor, thus allowing the female to expend more energy for ova production. As stated in previous sections, sex ratio was dependent on the number of parasites per host egg.

Effect of Photophase

Median or 50th percentile durations and standard errors of T. pretiosum life stages and developmental time from oviposition to

50% adult emergence when reared under three photophases are presented in Table 10. Photophase is not commonly associated with an increase or decrease in length of development. A review by Saunders (1979) cited instances where growth rate was influenced by photophase. Denlinger (1972) suggested that lengthened development in short-day larvae was because the larvae were diapause-committed. Saunders (1971) felt that photoperiod was responsible for lengthened development, but interacted with temperature to raise the incidence of diapause (i.e., more short-day cycles are seen before the end of the sensitive period). Research conducted in Texas suggests that T. pretiosum does not enter a true state of diapause, but overwinters as immatures at a reduced rate of development (Lopez and Morrison, 1980). The method of T. pretiosum overwintering in Kansas is not known. However, if T. pretiosum does diapause in Kansas, Saunders' hypothesis would help explain the lengthened developmental time observed under a 12-hour photophase. Photophase-temperature interaction studies are needed to better understand the photophase-developmental time relationship. A 12-hour photophase does not occur during the second generation SWCB oviposition period. An increase in developmental time under the 16-hour photophase was probably caused by pupae missing an eclosion gate and experimental variation. Eclosion rhythms have been observed for T. semifumatum (Rounbehler and Ellington, 1973).

Table 11 shows male, female, and average adult longevity when reared under three photophases. Longevity was significantly ($P < 0.05$) shorter when T. pretiosum were reared under a 12-hour photophase. Although the 14-hour and 16-hour photoperiod longevities were not

Table 10. Median or 50th percentile durations and standard errors (Days)^a of T. pretiosum

Riley life stages when reared under three photophases.

Photophase (hr)	Egg	Larval	Prepupal	Pupal	Oviposition- Adult
12	1.25 \pm 0.13	1.00 \pm 0.16	3.36 \pm 0.16	4.92 \pm 0.29	10.53 \pm 0.26
14	0.91 \pm 0.06	1.32 \pm 0.37	2.70 \pm 0.21	2.87 \pm 0.34	7.80 \pm 0.23
16	0.67 \pm 0.18	1.97 \pm 0.22	2.65 \pm 0.18	3.86 \pm 0.20	9.15 \pm 0.10

^a50% of the population completed the stage in this time period.

Table 11. T. pretiosum Riley longevity (days) after adult emergence when reared under three photophases.^a

Photophase (hr.)	Male Longevity	Female Longevity	Average Longevity
12	0.70 a	0.75 a	0.73 a
14	1.30 a	1.83 b	1.72 b
16	1.94 a	2.43 b	2.17 b

^aNumbers followed by the same letter in the same column are not significantly different ($P>0.05$) using Duncan's New Multiple Range Test.

Table 12. T. pretiosum Riley female fecundity and sex ratio when reared under three photophases.^a

Photophase (hr.)	Fecundity	Sex Ratio ^b
12	10.43 a	.588
14	9.85 a	.732
16	8.50 a	.438

^aNumbers followed by the same letter in the same column are not significantly different ($P > 0.05$) using Duncan's New Multiple Range Test.

^bNumbers represent the female proportion of the population.

significantly different, there appeared to be a general trend of increased longevity with a lengthened photophase. Rounbehler and Ellington (1973) showed a general increase in life span of T. semifumatum females as photophase lengthened.

Female fecundity and sex ratio are presented in Table 12. Fecundity was not significantly ($P > 0.05$) affected by photophase. Sex ratio was not influenced by photophase, but varied with the number of parasites per host egg.

Seasonal Occurrence

Cumulative completion of the SWCB moth flight and oviposition during 1978 and 1979 are plotted in Figures 7 and 8. Percent completion of Trichogramma parasitism was included on the 1979 plot. Low SWCB densities during 1978 decreased the chance of picking up parasitized SWCB eggs when sampling. Also, since T. pretiosum are density-dependent, the probability of locating a host was decreased. No parasitism of SWCB eggs was seen during 1978. Although 1978 and 1979 weather conditions (Appendix VIII) were considerably different, the rate of oviposition was similar. Fifty percent completion of oviposition occurred on 5 August 1978 and 8 August 1979. However, warm spring temperatures during 1977 shifted the peak SWCB moth flight two weeks earlier than in 1976 (Schenk, 1978). The first parasitized SWCB eggs were observed on 1 August 1979.

Field populations of SWCB females laid on the average 2.05 eggs/mass. Parasitized SWCB eggs averaged 2.93 eggs/mass. Schenk (1978) reported an average of between two to three SWCB eggs/mass. In all but

Figure 7. Southwestern corn borer moth flight and oviposition rates during 1978 at Sandyland Experiment Field, St. John, Kansas.

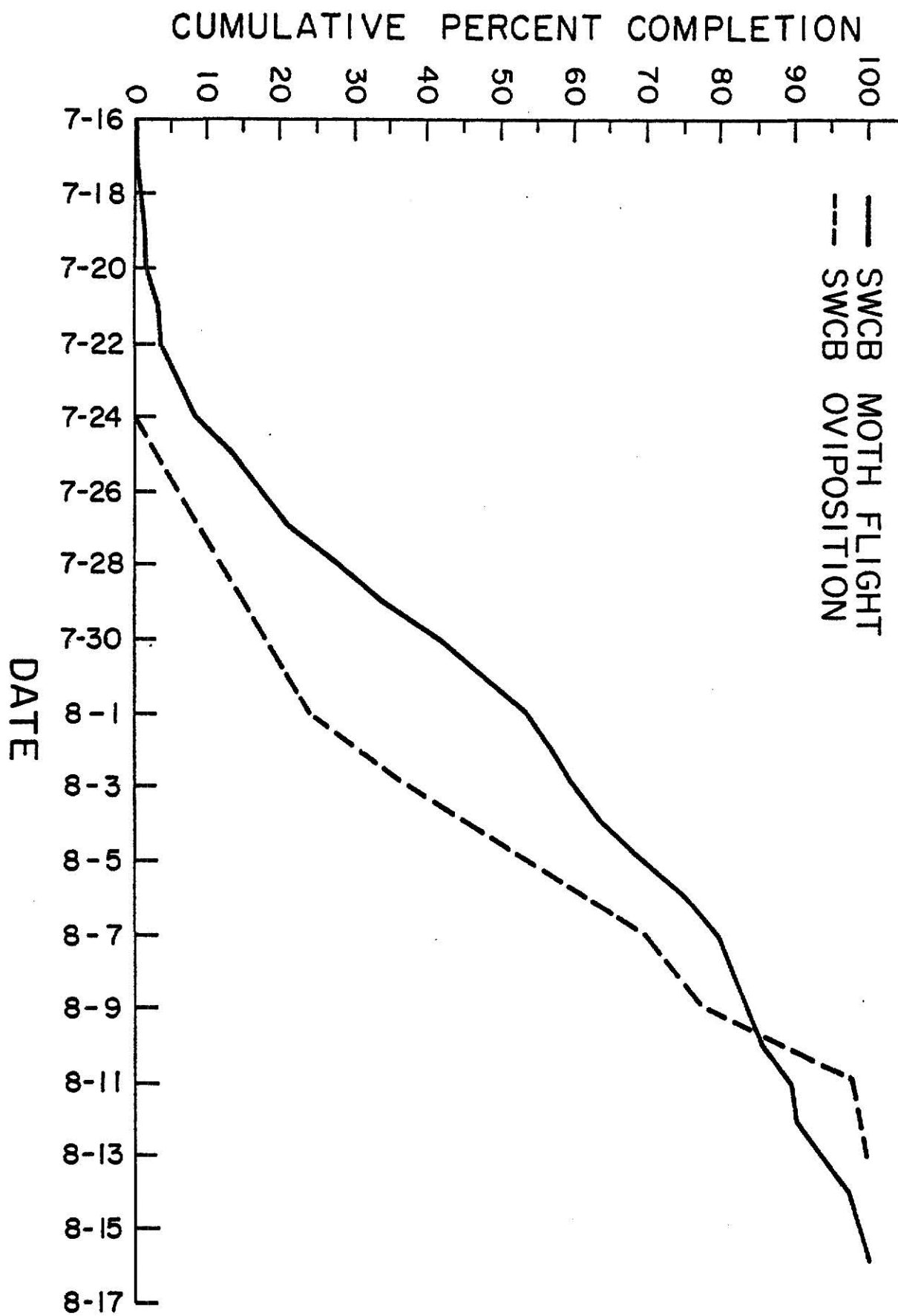
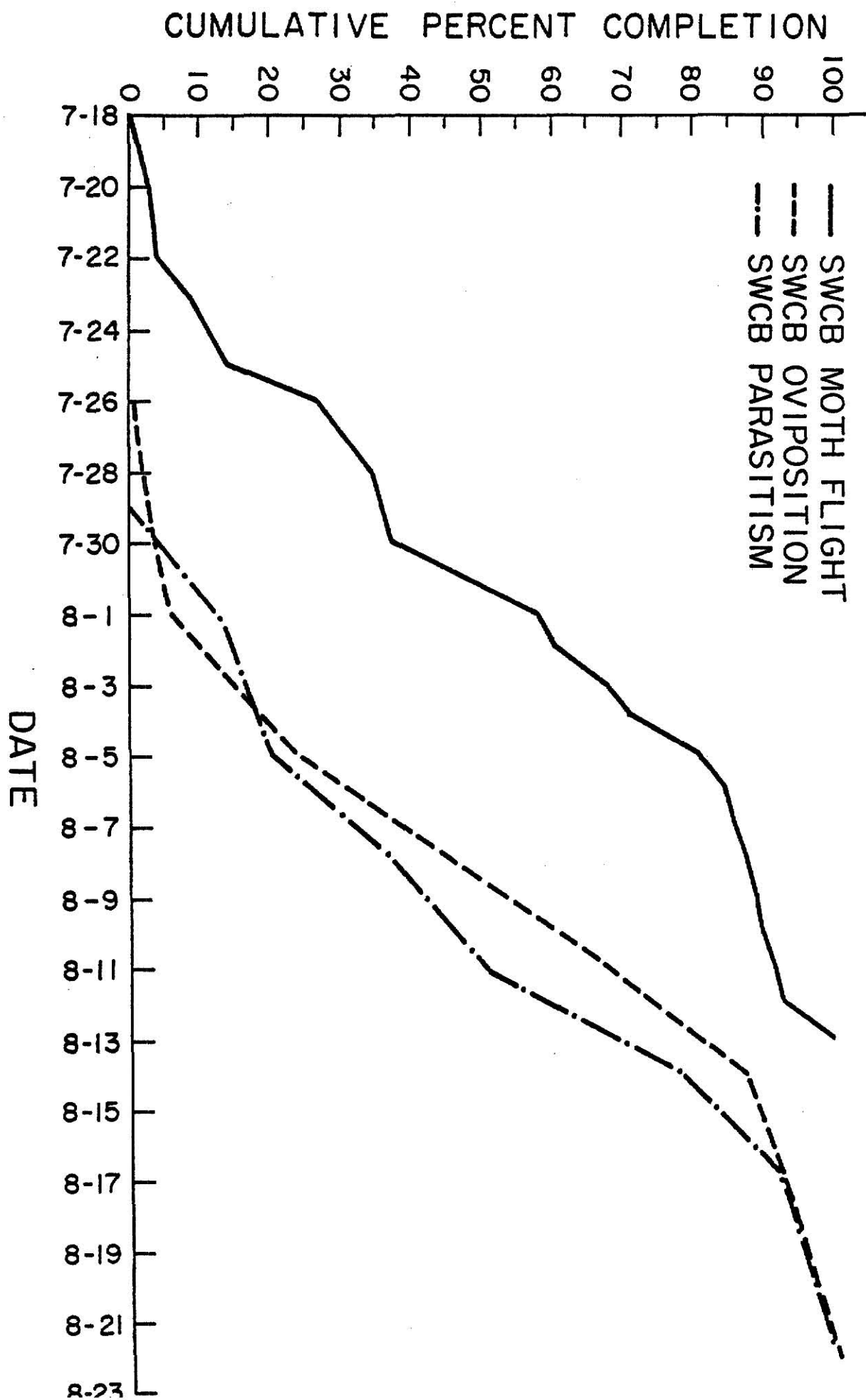


Figure 8. Southwestern corn borer moth flight and oviposition rates and rate of egg parasitism by Trichogramma Spp. during 1979 at Sandyland Experiment Field, St. John, Kansas.



one case, all SWCB eggs in a mass were parasitized. Because Trichogramma are extremely small and disperse poorly, oviposition in all host eggs in a mass would be advantageous. However, over-parasitism would create intraspecific competition for available food. Field parasitized SWCB eggs average 2.79 Trichogramma per SWCB egg with a range of one to four parasites per host egg. Laboratory parasitized SWCB eggs averaged approximately three ($\bar{x} = 2.92$) parasites per host egg, but range from one to nine parasites per host. Under natural conditions, Trichogramma probably seldom oviposit more than four ova per host egg. Laboratory data indicated that 85.5% of parasitized host eggs contained four or less developing parasites. Host eggs containing five or more parasites are believed due to adult over-crowding. The sex ratio of field collected Trichogramma was .750 (number of females/males + females).

If, on the average, three Trichogramma ova are deposited per SWCB egg and each SWCB egg mass parasitized averages three eggs, each female Trichogramma would have the opportunity to deposit nine ova per SWCB egg mass. Interestingly, when reared at temperatures between 25°C and 35°C, average female fecundity was nine ova/female. At temperatures below 25°C, each female averaged approximately 18 eggs. Therefore, a female Trichogramma may only need to encounter one or two SWCB egg masses to deposit all of her potential progeny.

Parasitism of the naturally occurring SWCB egg population during 1979 was 12.25% compared to 7.25% for the artificially infested egg population (Table 13). Substrate differences (artificially infested eggs were on wax paper discs) may have caused differential parasitism

Table 13. Comparison of natural and artificial SWCB egg population mortality during 1979 at Sandyland Experiment Field.^{ab}

	Natural Infestation	Artificial Infestation
Total Number of SWCB Eggs	302.00	248.00
Number of Egg Masses	147.00	118.00
Average Number of Eggs/Mass	2.05	2.10
Number of Eggs Parasitized	37.00	18.00
% Parasitism	12.25 (8.90-16.37)	7.26 (4.46-11.15)
% of Eggs Missing	3.31 (1.71-5.91)	41.94 (35.85-48.23)
% of Eggs Desiccated	0.66 (0.15-2.30)	4.44 (2.30-6.60)
% Egg Hatch ^c	83.78 (79.92-88.31)	46.36 (40.15-52.66)

^aBased on samples taken from a 121.9 x 330.5 m sample universe located at St. John, Kansas.

^bNumbers in parentheses are 95% confidence limits for percentages (Rohlf and Sokal (1969), pp. 208-214).

^cMissing eggs may have hatched before they disappeared.

because of attractiveness to the searching female. However, differences in percent parasitism between natural and artificial egg populations could have been caused by artifacts in the rate of artificial infestation. Logistics made daily field placement of laboratory reared eggs infeasible (SWCB colony was located at Manhattan, Kansas). All artificially infested eggs were placed in the field after peak oviposition of the natural population (see Figure 8). The greatest difference between the natural and artificial SWCB egg population was the percent of missing eggs. Approximately 42% of the artificially infested eggs were missing versus 3% of the naturally occurring SWCB egg masses. Missing eggs were probably the result of predation or desiccation and egg droppage from the plant. Straight pins were used to secure the wax paper discs to the upper surface of the plant leaf. Artificially infested eggs may have been dislodged by wind, rain, or birds. Greater percent desiccation of artificially infested eggs was probably due to hotter temperatures on the white paper discs.

Theoretical Model

The outcome (percent parasitism) of all possible combinations of model input variables and parameters are shown in Appendix IX. To determine if the model was behaving reasonably, 1979 field parasitism was compared to a model run with similar conditions.

Trichogramma parasitism during the 1979 second generation SWCB oviposition period was 12.25%. Field samples indicated that 96,000 SWCB eggs/acre were laid during the 1979 second generation SWCB oviposition period. Based on known T. pretiosum fecundity and

population samples, the initial T. pretiosum population was predicted to be 300 wasps/acre. Both immature parasite mortality and the probability of locating a host were unknown. However, personal observation in the laboratory and field indicates that immature mortality is probably 25% or less.

The simulation that most closely fit the 1979 field conditions predicted 14.22% parasitism. The simulated conditions were:

(1) immature parasite mortality--25%; (2) probability of locating a host--50%; (3) initial adult parasite population--500 parasites/acre; and (4) seasonal second generation SWCB egg population--96,000 SWCB eggs/acre. The model appeared to adequately simulate T. pretiosum parasitism based on the 1979 data. However, more seasons of data are needed to further define the range in which the model behaves adequately.

Predicted percent parasitism using two augmentation programs and no augmentation are presented in Table 14. A high, medium, and low predicted percent parasitism were chosen to represent the range of conditions simulated by the model. Within the range of conditions simulated, T. pretiosum did not appear to adequately reduce SWCB egg populations naturally. Under the best conditions only 50.7% of the second generation SWCB eggs were parasitized. The poorest conditions resulted in only 0.04% parasitism. Two releases of 2000 parasites/acre resulted in 96.8% parasitism under the best conditions. However, under the poorest conditions, one augmentation of 2000 parasites/acre increased parasitism from 0.04% to 1.4%.

Table 14. Predicted percent parasitism for selected model runs using two augmentation programs and no augmentation.

Immature <u>T. pretiosum</u> Mortality (%)	Probability of Locating a Host (%)	Initial Adult Female <u>T.</u> <u>pretiosum</u> Population (#/acre)	SWCB Egg Population (#/acre)	No Aug- mentation	Percent Parasitism					
					Program 1 ^a			Program 2 ^b		
					500	1000	2000	500	1000	2000
25%	75%	500	48,000	50.7	65.3	78.1	90.1	79.5	91.6	96.8
25	75	500	96,000	42.2	51.2	59.7	73.9	60.7	75.3	90.9
25	75	500	192,000	21.5	26.0	30.5	39.5	35.0	48.5	67.3
50%	50%	500	48,000	12.9	19.0	25.0	37.2	27.4	41.9	55.8
50	50	500	96,000	7.4	10.5	13.5	19.6	14.7	21.9	36.4
50	50	500	192,000	3.7	5.2	6.8	9.8	7.3	11.0	18.2
75%	25%	50	48,000	0.16	1.5	2.8	5.5	2.9	5.7	11.2
75	25	50	96,000	0.08	0.7	1.4	2.8	1.5	2.8	5.6
75	25	50	192,000	0.04	0.4	0.7	1.4	0.7	1.4	2.8

^aNumber of T. pretiosum adult females released 7 days after the simulation began.

^bNumber of T. pretiosum adult females released 4 and 8 days after the simulation began.

According to the model, one release of 2000 parasites/acre seven days after model initiation reduced SWCB egg populations approximately equal to two releases of 1000 parasites/acre four and eight days after model initiation. This indicates that a grower could possibly save time and energy by releasing parasites once at twice the rate.

The predicted seasonal T. pretiosum age distributions for three simulations are shown in Figures 9, 10, and 11. Under the defined set of conditions, T. pretiosum completed two generations (approximately 11 days/generation) during the second generation SWCB oviposition period. Figure 9 represents a parasite population that is decreasing because mortality exceeded the natality rate. Under these conditions the population is moving toward extinction. Parasite releases to control SWCB egg populations would require large numbers of parasites and many releases. Figure 10 represents a parasite population that is maintaining a fairly constant level. This population resulted in 12.93% parasitism of the SWCB egg population. A parasite population that reduced the SWCB egg population 50.7% is shown in Figure 11. In this case, natality greatly exceeded mortality. Augmenting a population under this set of conditions would have the best chance of success.

The theoretical model was developed as a tool to evaluate the potential of T. pretiosum as a biological control agent of the SWCB. The model was not intended as an exact representation of the SWCB-T. pretiosum system. The model serves to point out the areas in the host-parasite system where knowledge is needed.

Figure 9. Predicted T. pretiosum life stage seasonal age distribution when mortality was 75%; probability of locating a host, 25%; initial T. pretiosum female population, 50/acre; and total SWCB egg population, 192,000/acre. High parasite mortality and difficulty in finding a host results in declining T. pretiosum populations.

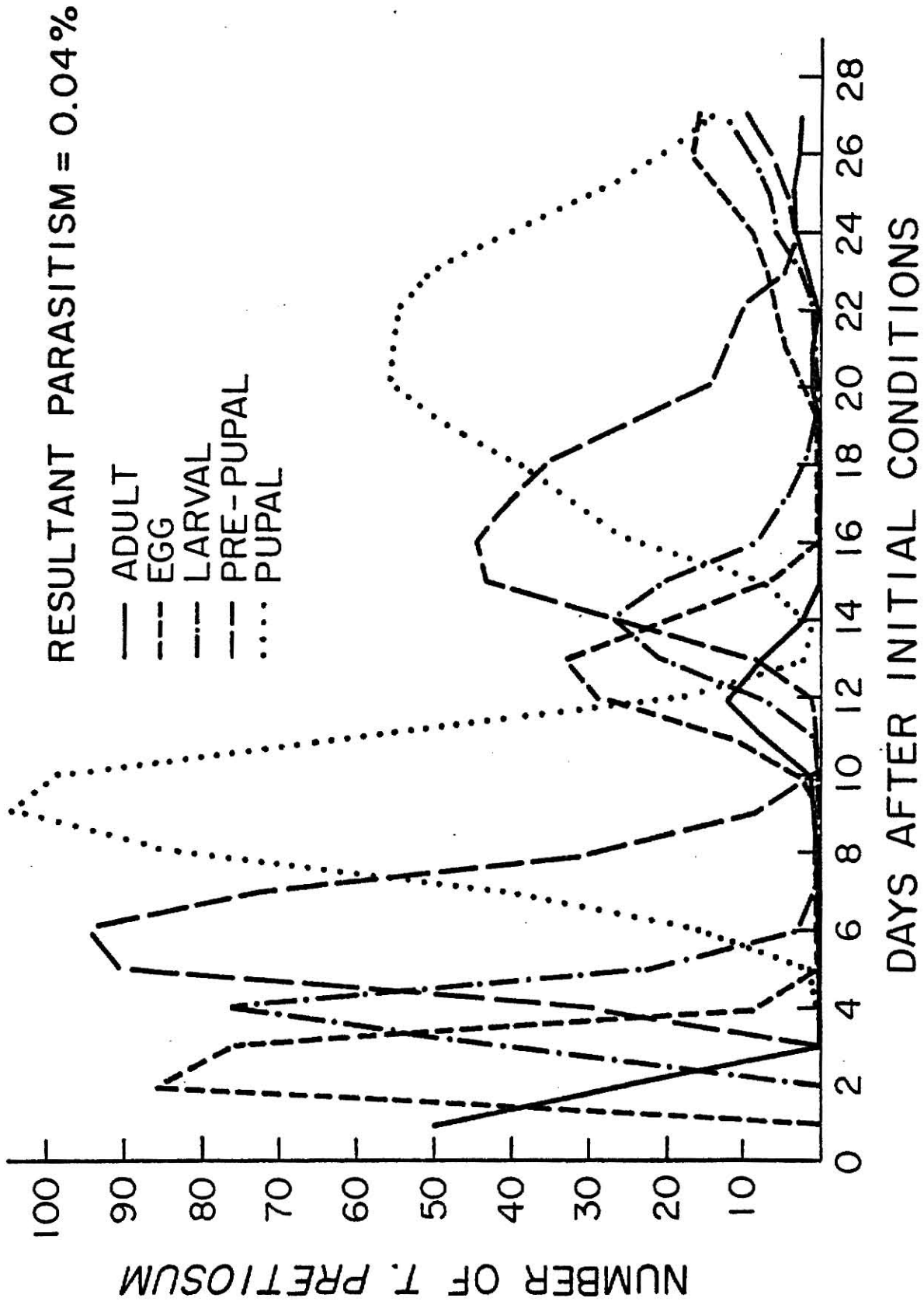


Figure 10. Predicted T. pretiosum life stage seasonal age distribution when mortality was 50%; probability of locating a host, 50%; initial T. pretiosum female population, 500/acre; and total SWCB population, 48,000/acre. Under these conditions, the parasite population shows slight increases.

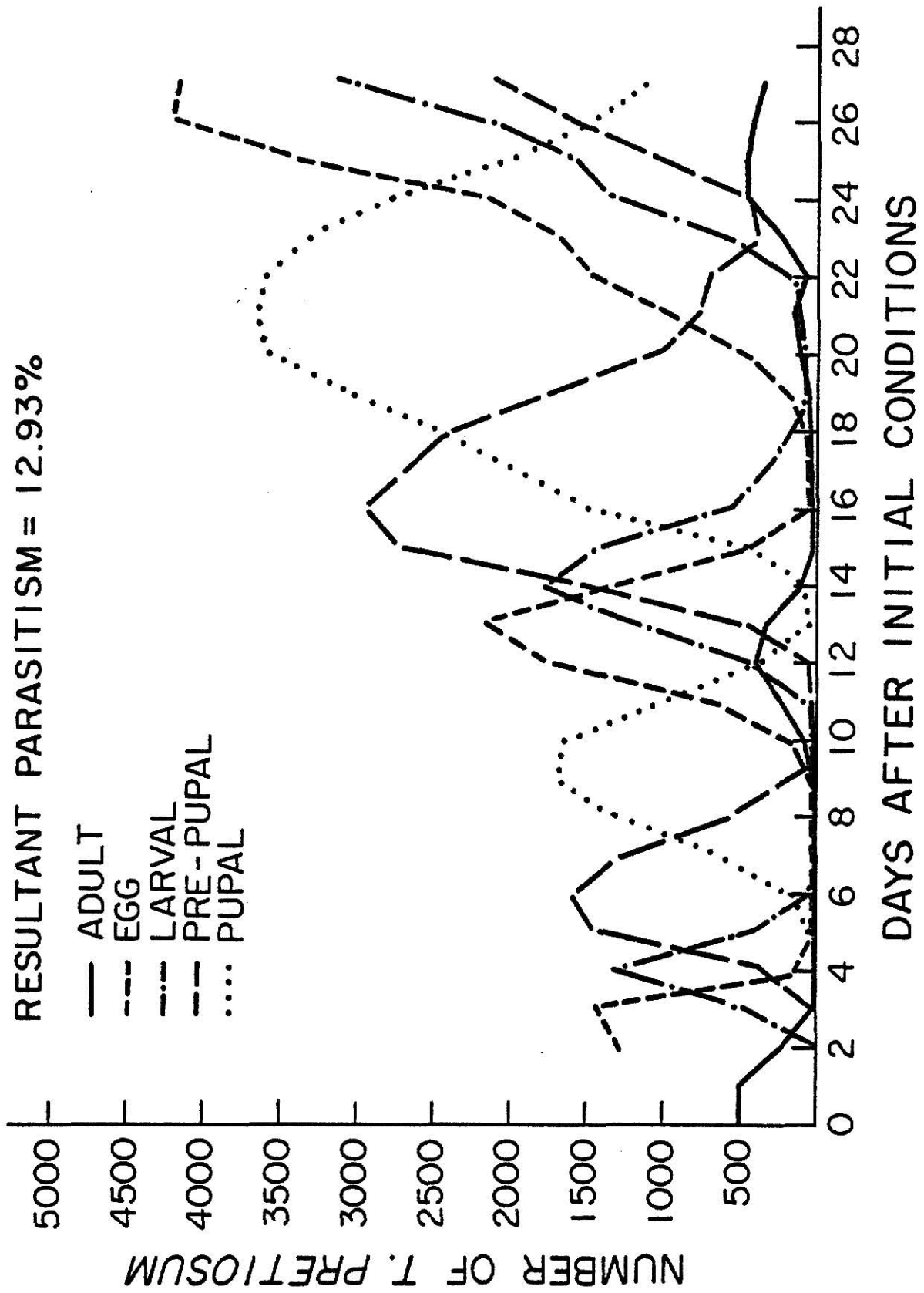
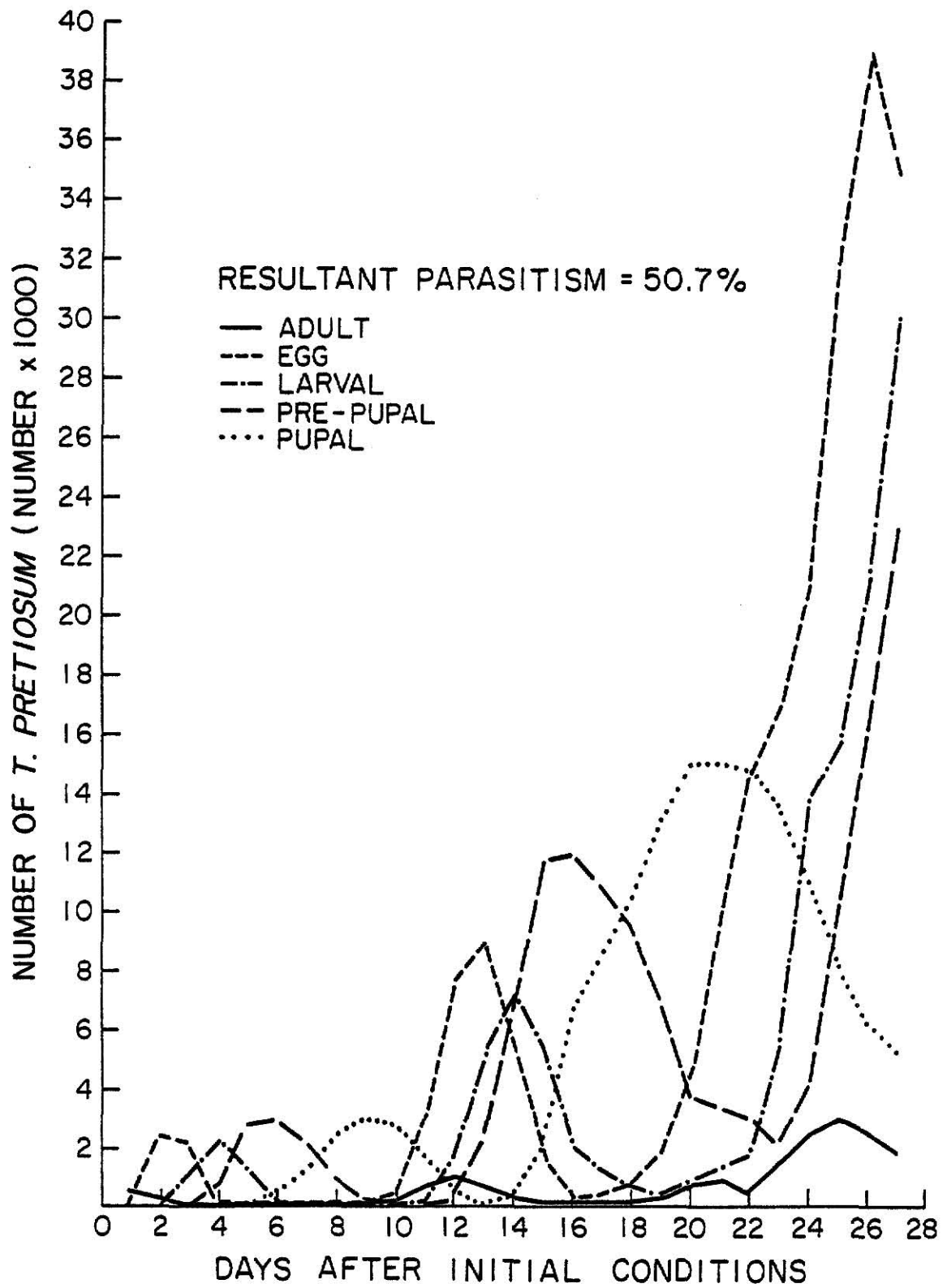


Figure 11. Predicted T. pretiosum life stage seasonal age distribution when mortality was 25%; probability of locating a host, 75%; initial T. pretiosum female population, 500/acre; and total SWCB egg population, 48,000/acre. Under these highly favorable assumptions, T. pretiosum populations would expand rapidly.



CONCLUSIONS

Developmental times for all life stages of T. pretiosum when reared at constant temperatures were described using second degree polynomial equations. Optimum developmental times were predicted to be 30°C for all life stages. However, the optimum temperature probably falls between 25°C and 35°C. Neither the number of parasites per host egg nor host volume were considered in determining the developmental time curves. Adult longevity was greatly increased at 17°C and significantly decreased at 35°C. Longevity was the same between 22°C and 30°C. T. pretiosum females reared at temperatures of 25°C and below contained twice as many ova as those reared at 30°C and 35°C. Sex ratio was influenced by the number of parasites per host egg and not temperature, humidity, or photophase. Fluctuating temperatures affected T. pretiosum developmental time very little when fluctuated within ranges commonly occurring during July and August in central Kansas. Fecundity and longevity were not affected by fluctuating temperatures.

Developmental time and longevity of T. pretiosum increased as relative humidity decreased. Developmental time and longevity were not significantly different above 60% RH. Although female parasites lived longer at low humidities, activity was less and fewer progeny were produced. Fecundity was twice as great at 80% RH as compared to 20% RH.

Data indicates that photophase may cause developmental time to increase as photophase decreases. Until research is conducted to investigate the effect of photophase-temperature interactions on T. pretiosum development, the nature of the relationship will remain unknown. Fecundity was not affected by photophase. A 12 hour photophase does not occur during July and August in Kansas. Therefore, lengthened development and shorter adult longevity caused by the 12 hour photophase is unimportant in determining the effect of T. pretiosum on second generation SWCB egg parasitism.

T. pretiosum parasitism appeared to follow SWCB second generation oviposition. Female wasps oviposit an average of three ova per SWCB egg and probably very seldom deposit more than four ova per host under field conditions. After locating a SWCB egg mass, female wasps usually oviposit in all eggs of the mass. Significantly more naturally occurring host eggs were parasitized than artificially infested host eggs. The largest difference in SWCB egg survivorship between natural and artificial infested eggs was missing eggs (dislodged by wind, rain, and/or predation).

Model behavior indicates that T. pretiosum probably cannot effectively control second generation SWCB egg populations naturally. Under assumptions which resulted in a decline in natural T. pretiosum populations, augmentation programs were ineffective. However, under more favorable assumptions, augmenting the parasite population appeared to efficiently reduce SWCB egg populations. Because model assumptions influence the predicted level of parasitism, it is important to quantify the range of values assumed for each variable

and parameter. An important result of the model was to point out a need for more research to determine values for parasite mortality and probability of locating a host. Knowing these values would indicate if conditions were conducive to effective augmentation of T. pretiosum populations to control SWCB egg populations.

Augmenting the parasite population once with twice as many parasites was as effective as two releases using half the number. T. pretiosum probably completes two generations during the second generation SWCB oviposition period. Based on 1979 field data, the model appeared to adequately simulate T. pretiosum parasitism. However, more seasons of data are needed to further define the model limits.

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APPENDIX I--K values for T. pretiosum life stages and SWCB egg stage and a mathematical description of the model.

Table 15. K values for T. pretiosum life stages and SWCB egg stage.

Life Stage	K Value ^a
Egg	17
Larval	6
Prepupal	16
Pupal	25
SWCB Egg	24

^aK values were determined by the equation: $K = \bar{x}^2/s^2$; where \bar{x} is the mean and s^2 is the variance.

MATHEMATICAL DESCRIPTION OF THE MODEL

Mathematical relationships between T. pretiosum-SWCB system variables and parameters were written into a computer program using Fortran Watfiv. The system was composed of three major components: (1) environment, (2) T. pretiosum population, and (3) SWCB egg population.

Environmental factors considered in the model were maximum and minimum daily temperature. Field data were collected at Sandyland Experiment Field during 1979 in degrees Fahrenheit and converted to degrees Celsius.

Maximum daily temperature (C°) = $5./9. \times (\text{Maximum daily temperature } (F^{\circ}) - 32.)$

Minimum daily temperature (C°) = $5./9. \times (\text{Minimum daily temperature } (F^{\circ}) - 32.)$

Using maximum and minimum daily temperatures, daily thermal-units were calculated.

Thermal units = $(\text{Maximum daily temperature} + \text{Minimum daily temperature}/2.) - 10.$

If the minimum daily temperature was less than $10^{\circ}C$, then $10^{\circ}C$ was used as the minimum temperature. Average daily temperatures were used to calculate the developmental time of T. pretiosum life stages.

Average daily temperature = (Maximum daily temperature + Minimum daily temperature)/2.

The second system component was the T. pretiosum population. Developmental times of T. pretiosum life stages (egg, larval, prepupal, and pupal) were determined using second degree polynomial equations, with average daily temperature (ADT) as the independent variable:

$$\begin{aligned}\text{Egg} &= 12.337 - (0.728 \times \text{ADT}) + 0.012 \times (\text{ADT}^2) \\ \text{Larval} &= 15.248 - (0.922 \times \text{ADT}) + 0.015 \times (\text{ADT}^2) \\ \text{Prepupal} &= 44.519 - (2.939 \times \text{ADT}) + 0.051 \times (\text{ADT}^2) \\ \text{Pupal} &= 44.302 - (2.701 \times \text{ADT}) + 0.044 \times (\text{ADT}^2)\end{aligned}$$

Rates of change (numbers per day) of T. pretiosum life stages were expressed by the following equations:

$$\begin{aligned}\text{Egg population} &= \text{newly oviposited eggs} - \text{new larvae} \\ \text{Larval population} &= \text{new larvae} - \text{new prepupae} \\ \text{Prepupal population} &= \text{new prepupae} - \text{new pupae} \\ \text{Pupal population} &= \text{new pupae} - \text{new adults}\end{aligned}$$

Because only the female proportion of the population was important in the model, new adults were converted to new adult females,

$$\text{New adult females} = \text{new adults} \times .603 \times \text{immature mortality.}$$

Laboratory females constituted 60.3% of the population. Immature mortality was input as a parameter and used to reduce the population of new adults. The adult female population rate of change was calculated using the following formula:

Adult female population = new adult females - dead females

All rate variables were integrated using Euler integration with a 1/24 day time step. The adult female T. pretiosum population was moved through time using a discrete delay with 48 one-hour steps. All other T. pretiosum stages were moved through time using a time-varying distributed delay. A subroutine written by Manetsch and Park (1974) was used for this purpose. The subroutine is as follows:

```

SUBROUTINE VDEL (VIN, VOUT, R, DEL, DELP, DT, K)
DIMENSION R(1)
A = DT x K/DEL
V = VIN
DELD = (DEL - DELP)/DT x K
DELP = DEL
Do 1 I = 1, K
DR = R(I)
R(I) = DR + A x (V - DR x (1. + DELD))
1 V = DR
VOUT = R(K)
RETURN
END

```

To determine the number of new eggs entering the population and the number of SWCB eggs parasitized, T. pretiosum's oviposition rate was determined based on the following formula.

Female T. pretiosum oviposition rate = adult female population x (Trichogramma fecundity/Trichogramma longevity) x probability of locating a host

Trichogramma fecundity was set at 9 ova/female when the temperature was 27°C or above and 18 ova/female when the temperature was below 27°C. Because temperatures during July and August are normally between 22°C and 35°C, T. pretiosum longevity was assumed to be

two days. The number of SWCB eggs parasitized was equal to the female T. pretiosum oviposition rate/3, assuming three parasite eggs are laid per SWCB egg.

The final system component was the SWCB egg population. Rate of change in the SWCB egg population was integrated using Euler integration with a 1/24 day time step.

$$\text{SWCB egg population} = \text{newly laid SWCB eggs} - (\text{blackhead SWCB eggs} + \text{parasitized eggs})$$

The SWCB oviposition rate was determined by cumulative percent completion of egg laying, as determined by the 1979 field data (Figure 8). Percent daily completion of seasonal oviposition was calculated using the formula:

$$\text{Daily percent completion of oviposition} = \frac{\text{total oviposition completed} - \text{total percent completed through the previous day}}{\text{total number of SWCB eggs oviposited during the season}}$$

Daily oviposition was then calculated:

$$\text{Daily oviposition} = \text{daily percent completion of oviposition} \times \text{total number of SWCB eggs oviposited during the season}$$

The developmental time from oviposition to blackhead was expressed by the following formula:

$$\text{Developmental time} = 85. / \text{daily thermal-units}$$

Because two factors were subtracted from the SWCB egg population, a modification of Manetsch and Park's subroutine was written to move SWCB eggs through time.

```

SUBROUTINE VDEL2A (VIN, VOUT, R, DEL, DELP, DT, K, AR)
DIMENSION R(1)
KM1 = K - 1
A = DT x K/DEL
B = (1 - AR x DEL/K)
DELD = (DEL - DELP)/(DT x K) + 1
DELP = DEL
DO 1 I = 1, KM1
1 R(I) = R(I) + A x (B x R(I + 1) - R(I) x DELD)
R(K) = R(K) + A x (VIN - R(K) x DELD)
VOUT = R(1) x B
RETURN
END

```

The seasonal percent parasitism was calculated.

Percent parasitism = (total parasitism/seasonal SWCB egg population) x 100

A card deck of the model is available upon request.

APPENDIX II--Observed percent completion of T. pretiosum life stages
when reared under various environmental conditions.

Figure 12. Observed percent completion of T. pretiosum life stages when reared at 17°C, 60% RH, and 14 h photophase.

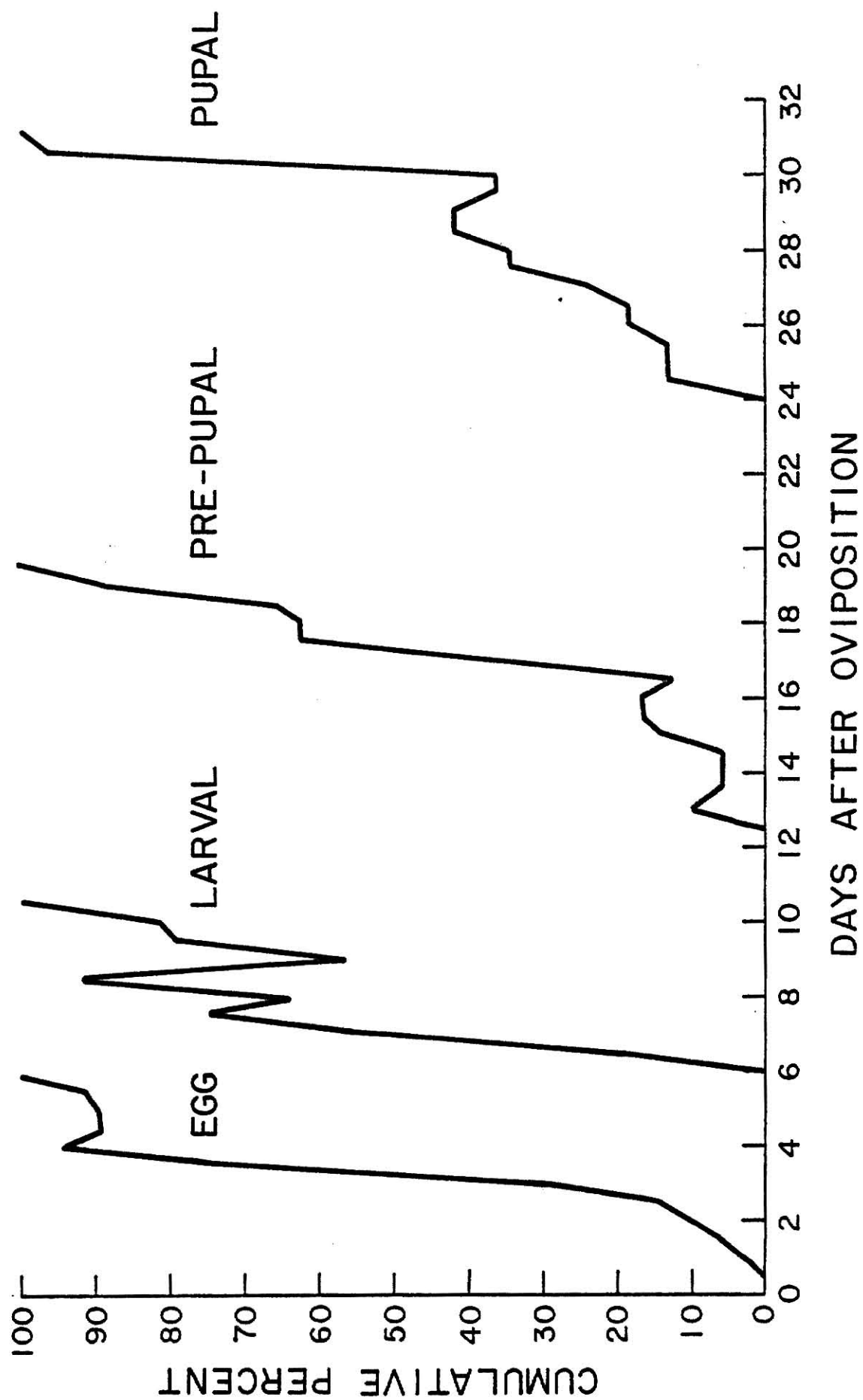


Figure 13. Observed percent completion of T. pretiosum life stages when reared at 20°C, 60% RH, and 14 h photophase.

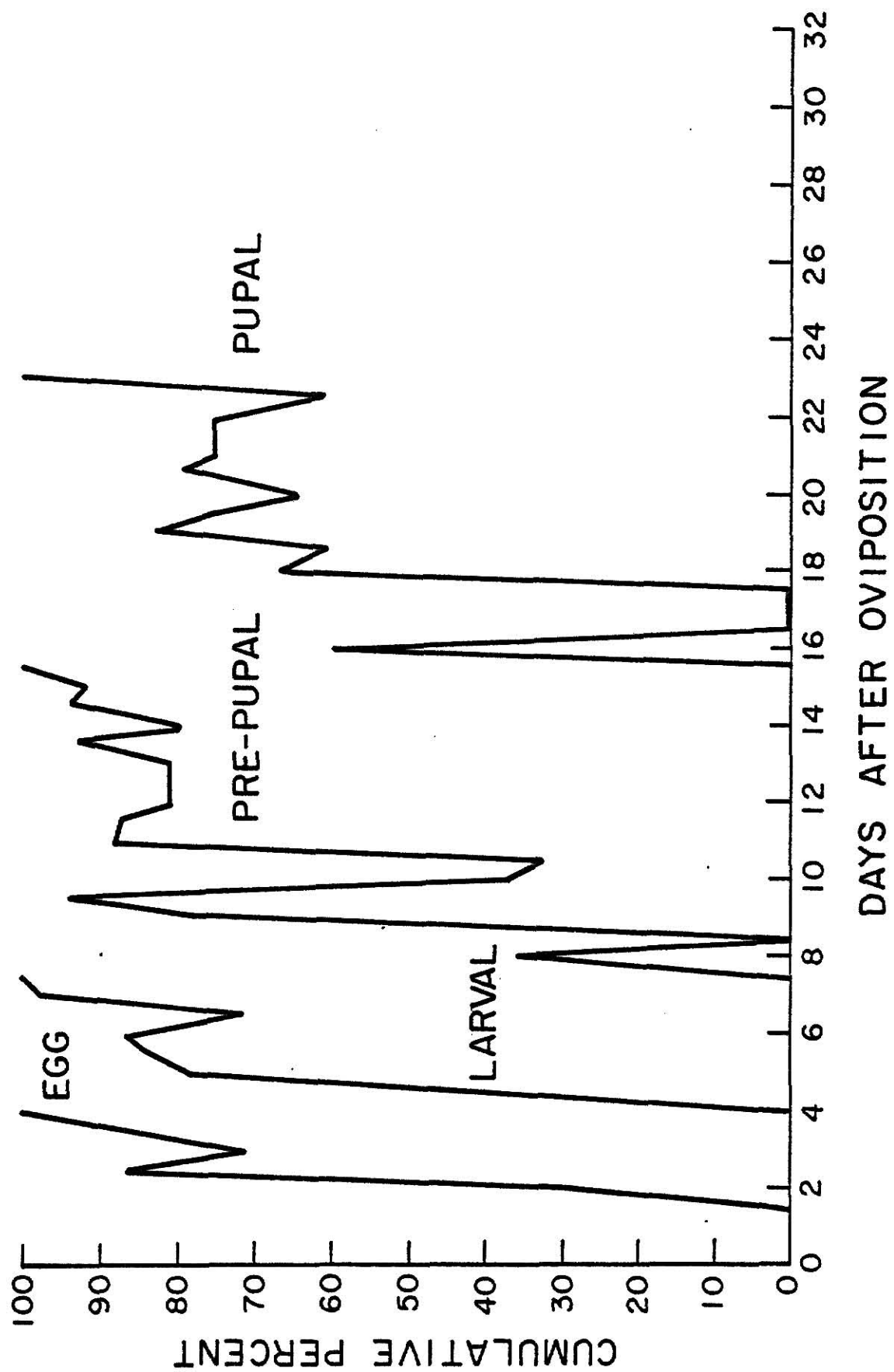


Figure 14. Observed percent completion of T. pretiosum life stages
when reared at 22°C, 60% RH, and 14 h photophase.

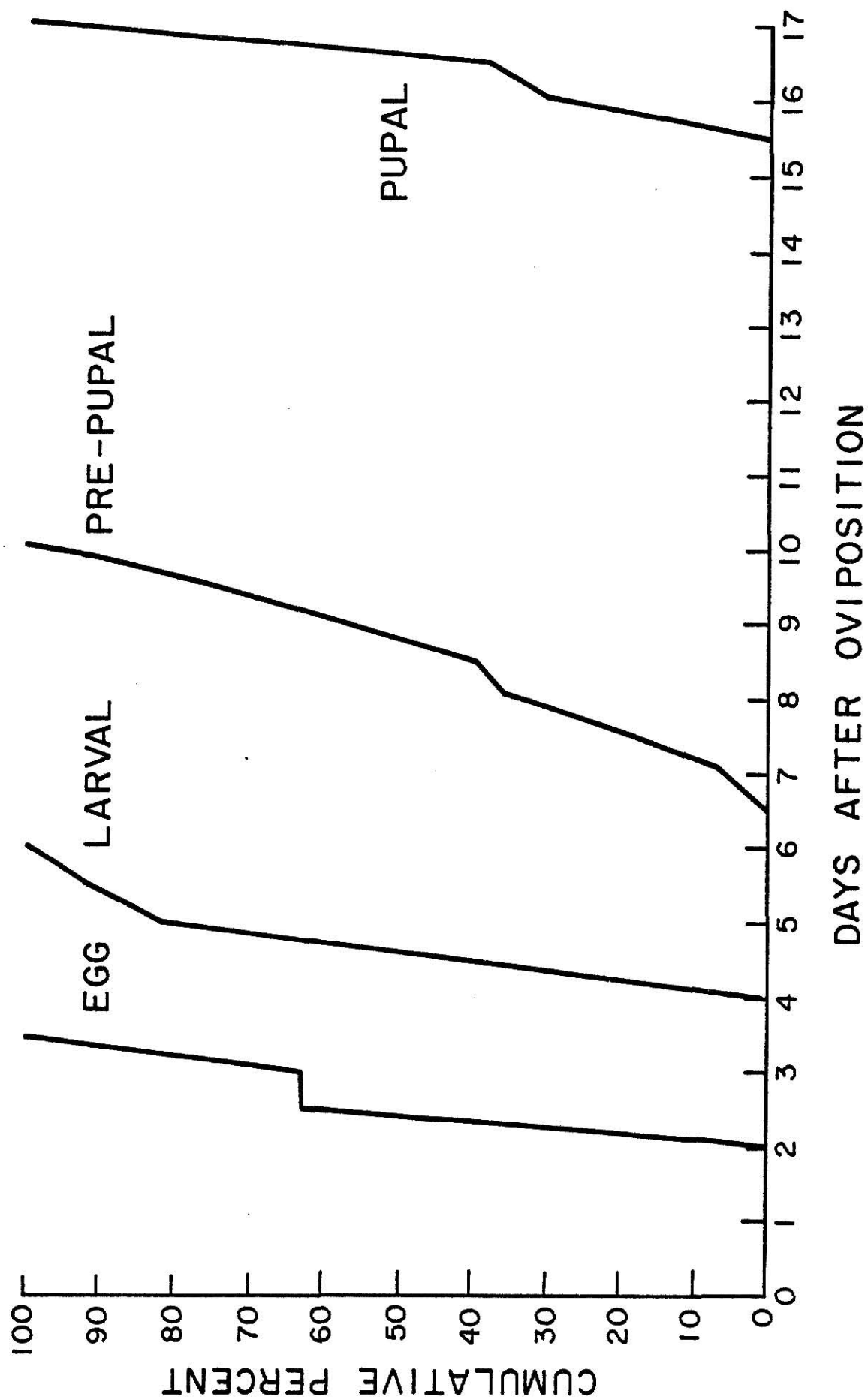


Figure 15. Observed percent completion of T. pretiosum life stages when reared at 25°C, 60% RH, and 14 h photophase.

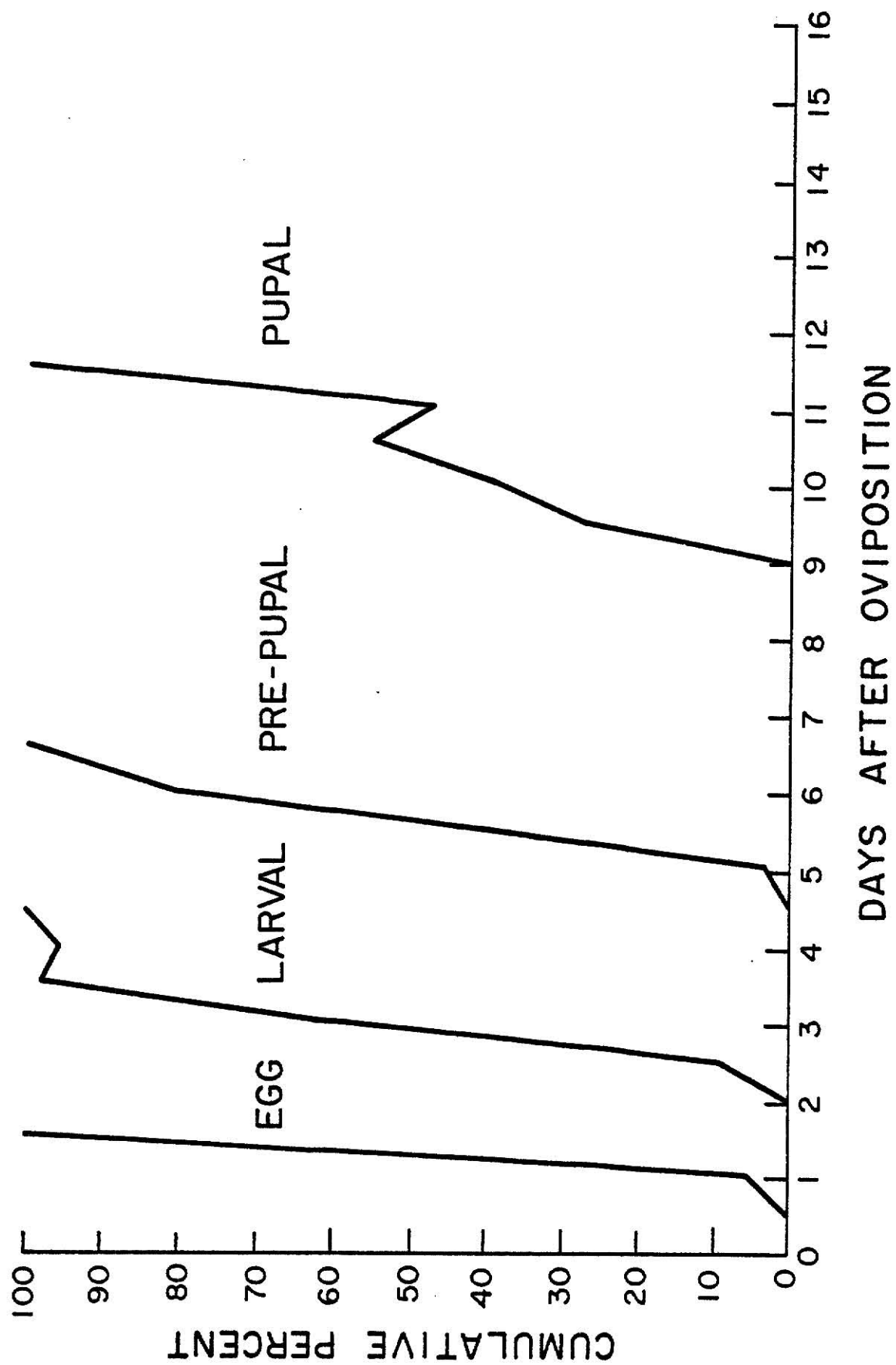


Figure 16. Observed percent completion of T. pretiosum life stages when reared at 30°C, 60% RH, and 14 h photophase.

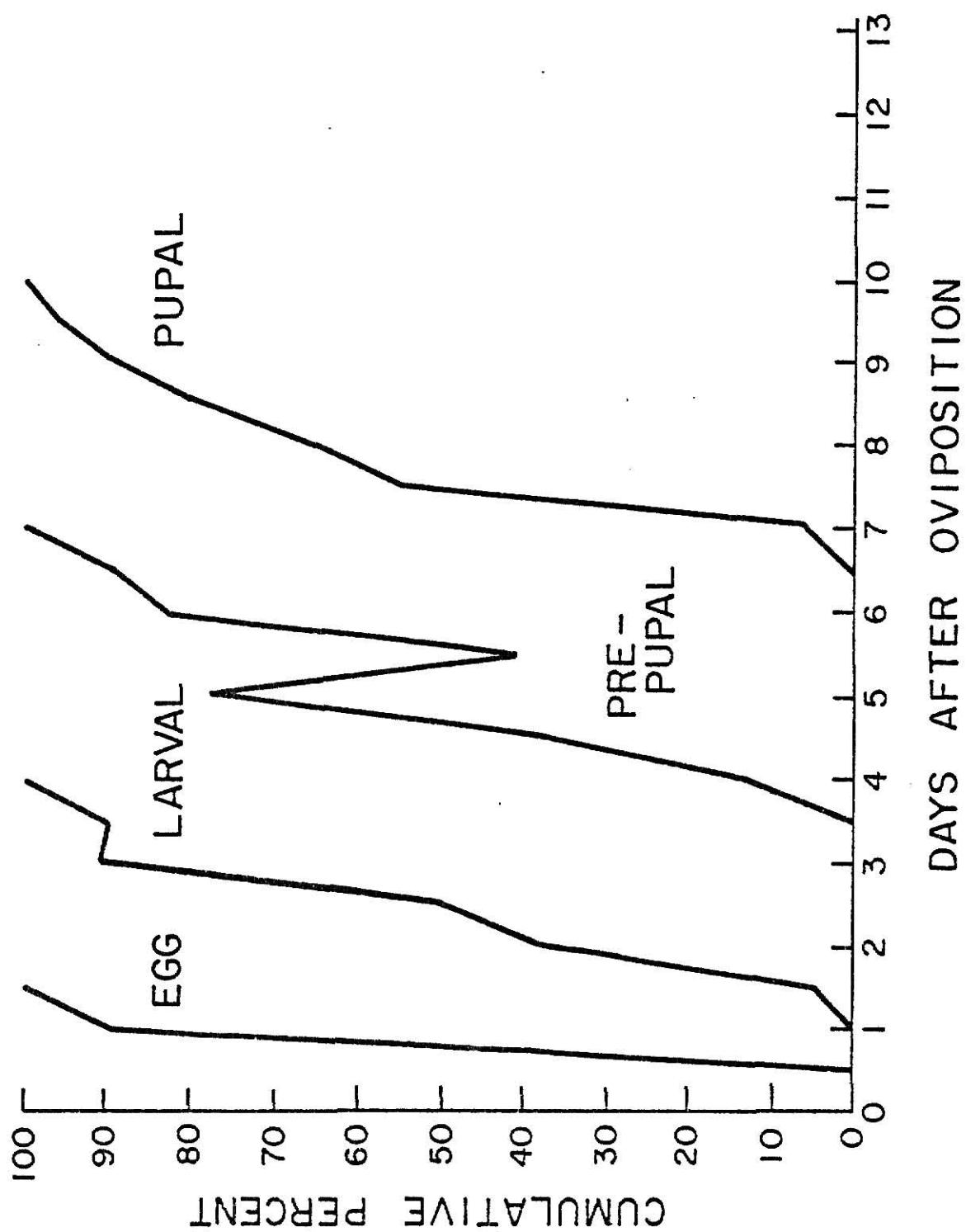


Figure 17. Observed percent completion of T. pretiosum life stages when reared at 35°C, 60% RH, and 14 h photophase.

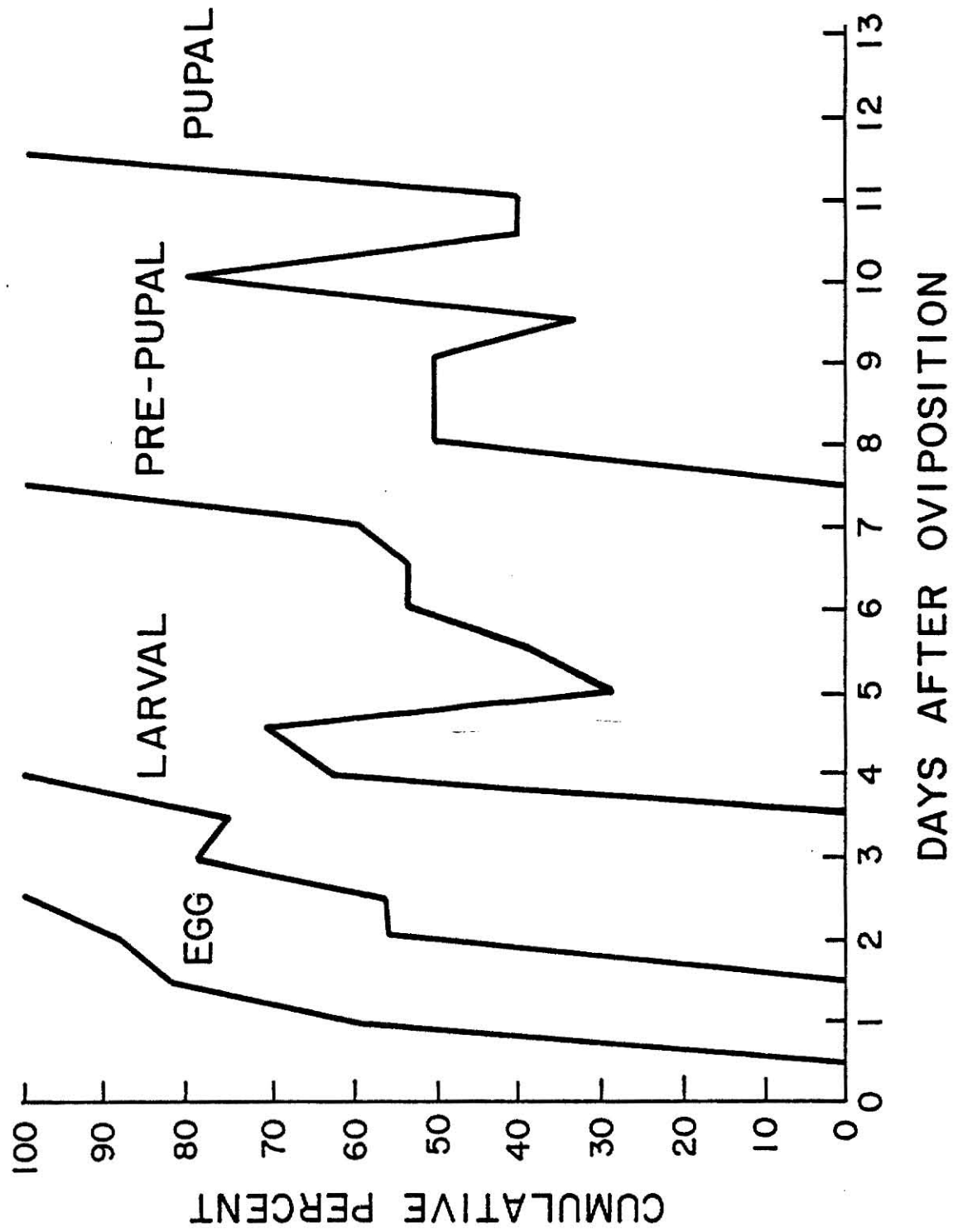


Figure 18. Observed percent completion of T. pretiosum life stages when reared at 28°C-32°C (\bar{x} = 30°C), 60% RH, and 14 h photophase.

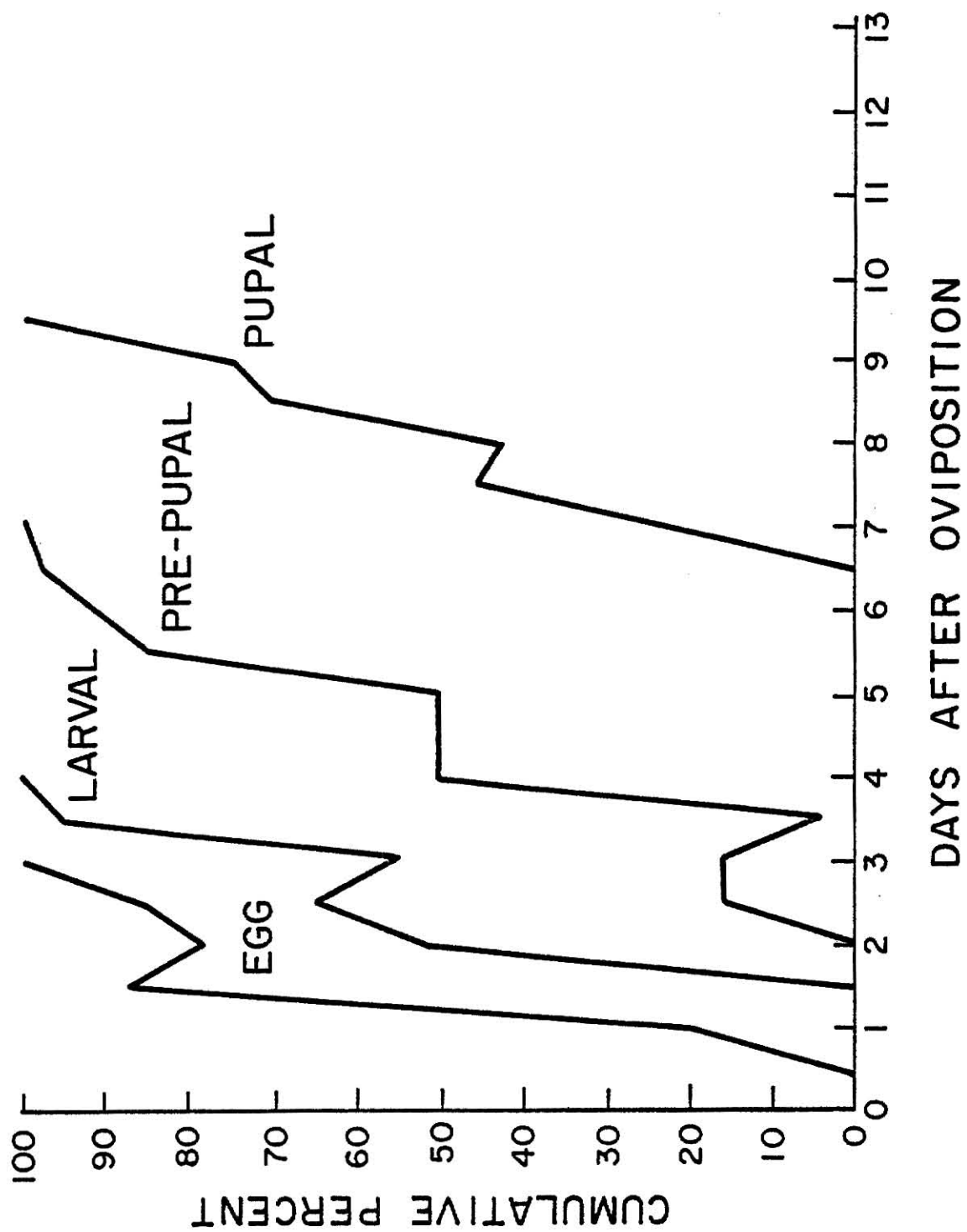


Figure 19. Observed percent completion of T. pretiosum life stages when reared at 26°C-34°C (\bar{x} = 30°C), 60% RH, and 14 h photophase.

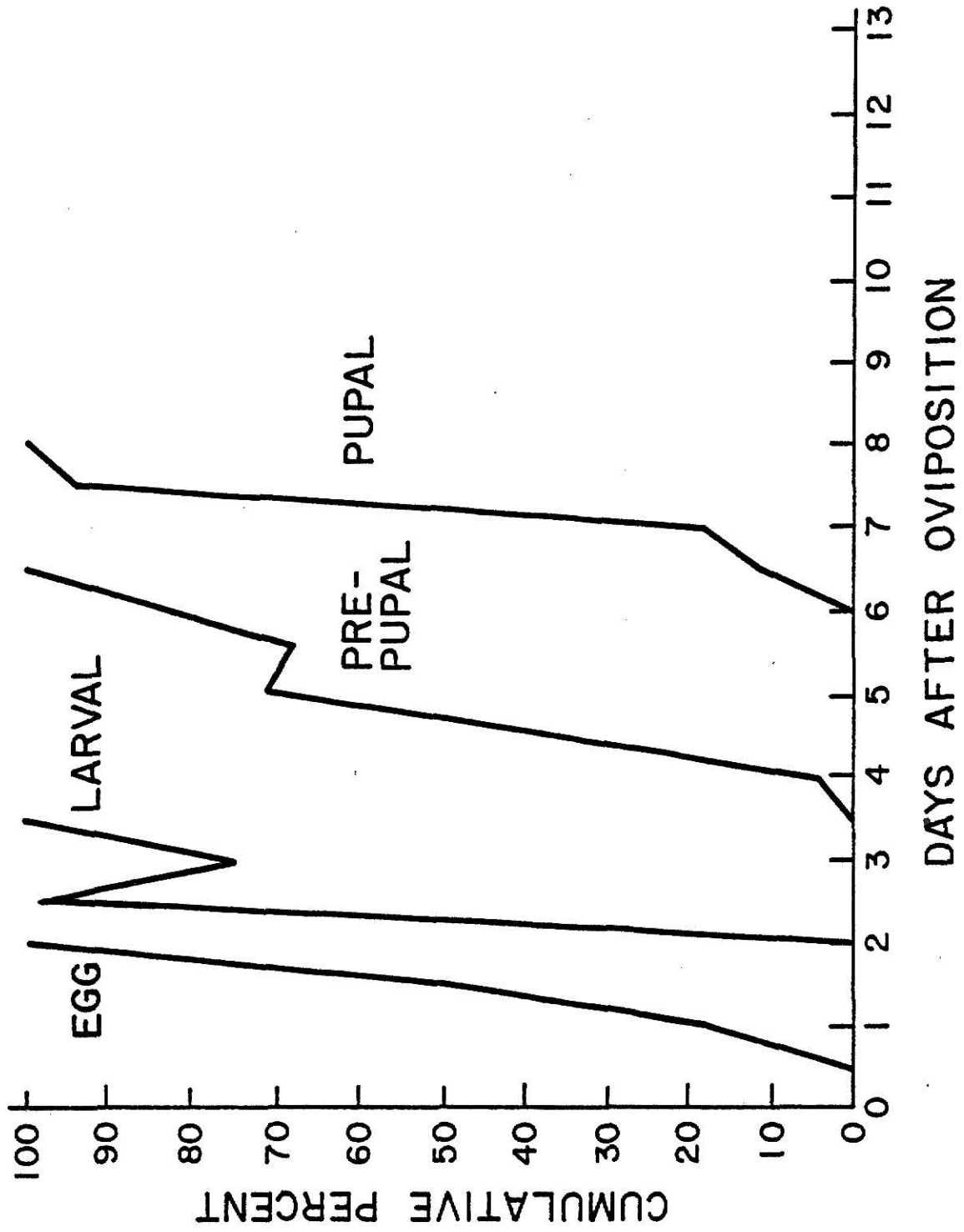


Figure 20. Observed percent completion of T. pretiosum life stages when reared at 22°C-38°C (\bar{x} = 30°C), 60% RH, and 14 h photophase.

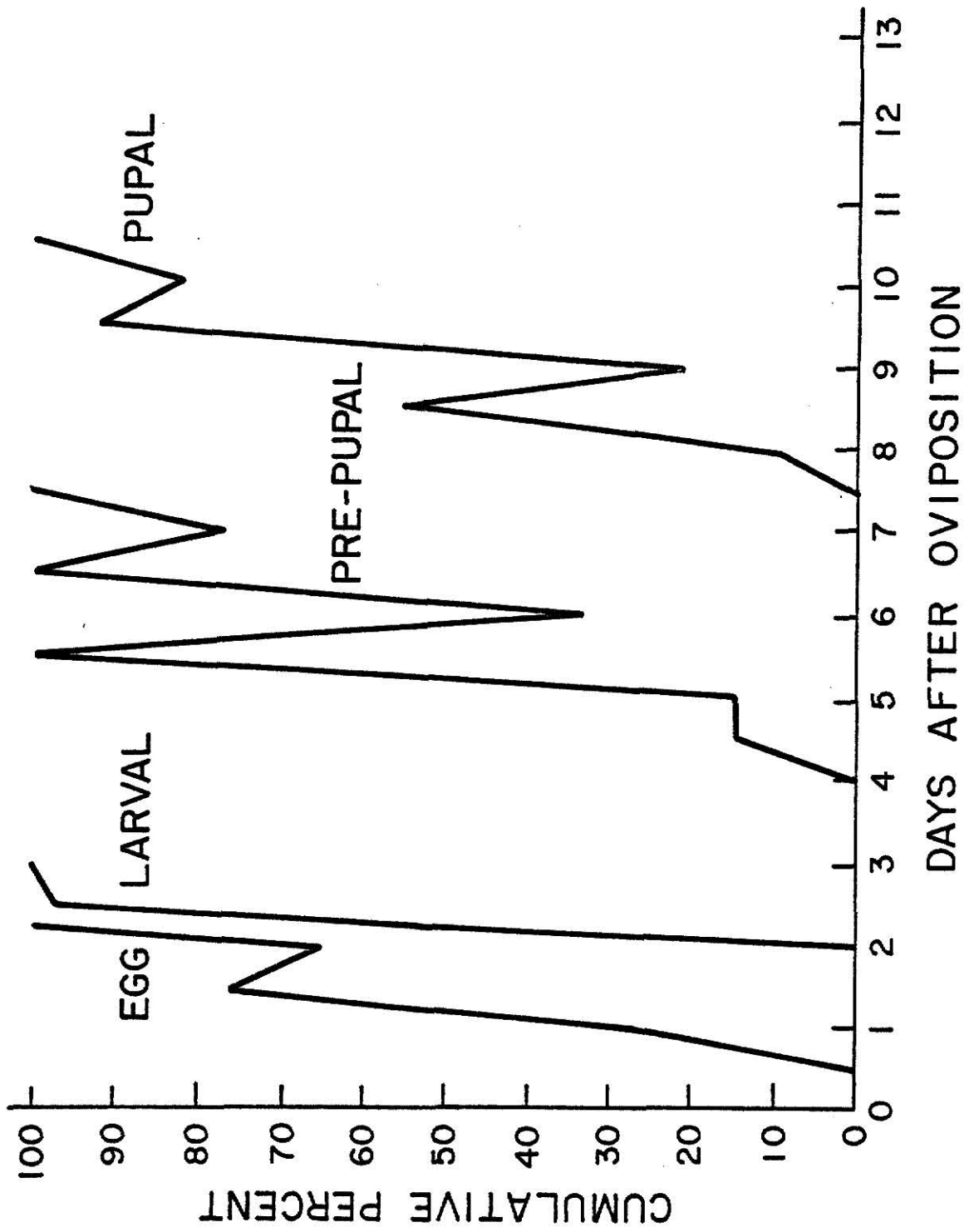


Figure 21. Observed percent completion of T. pretiosum life stages when reared at 30°C, 20% RH, and 14 h photophase.

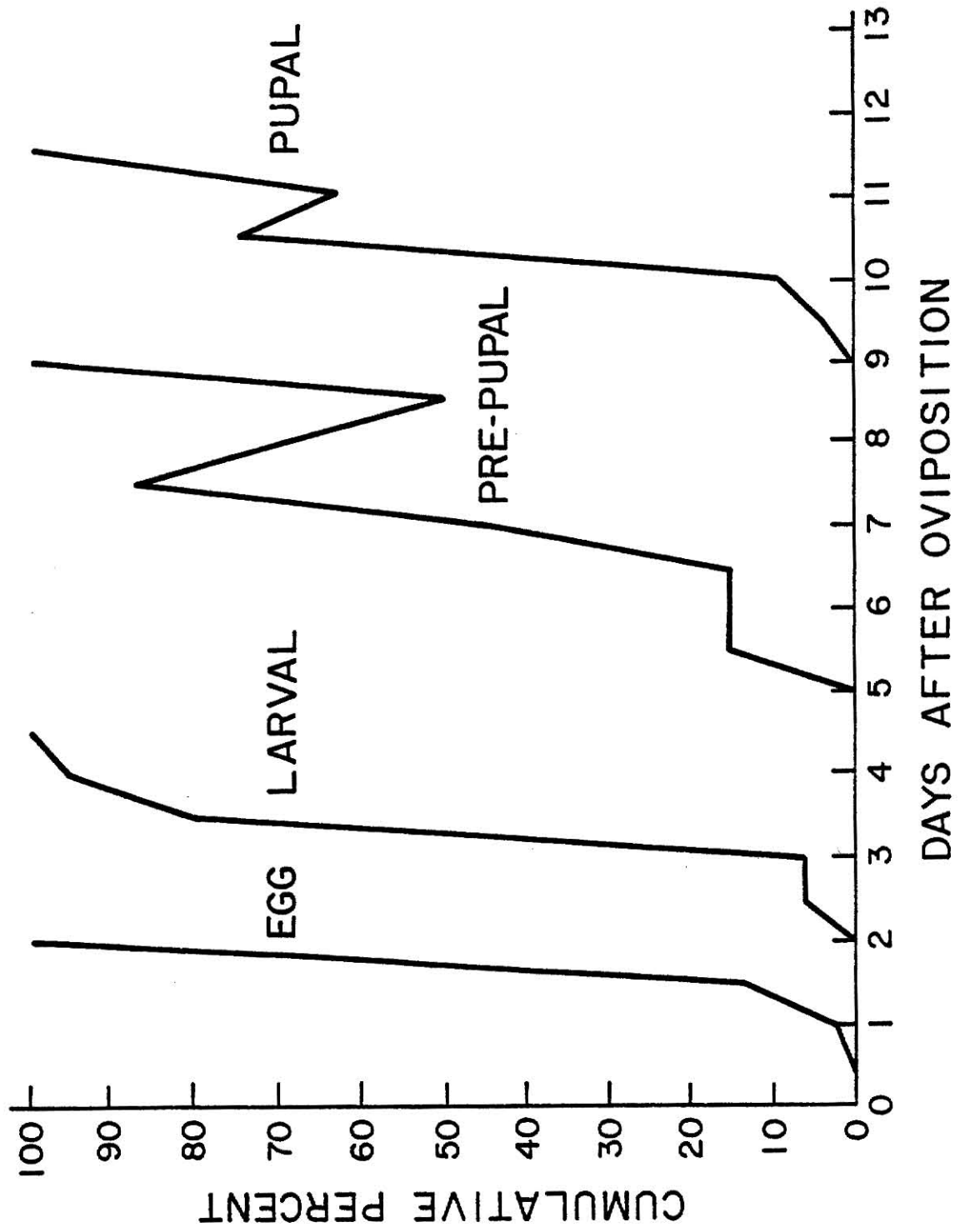


Figure 22. Observed percent completion of T. pretiosum life stages when reared at 30°C, 80% RH, and 14 h photophase.

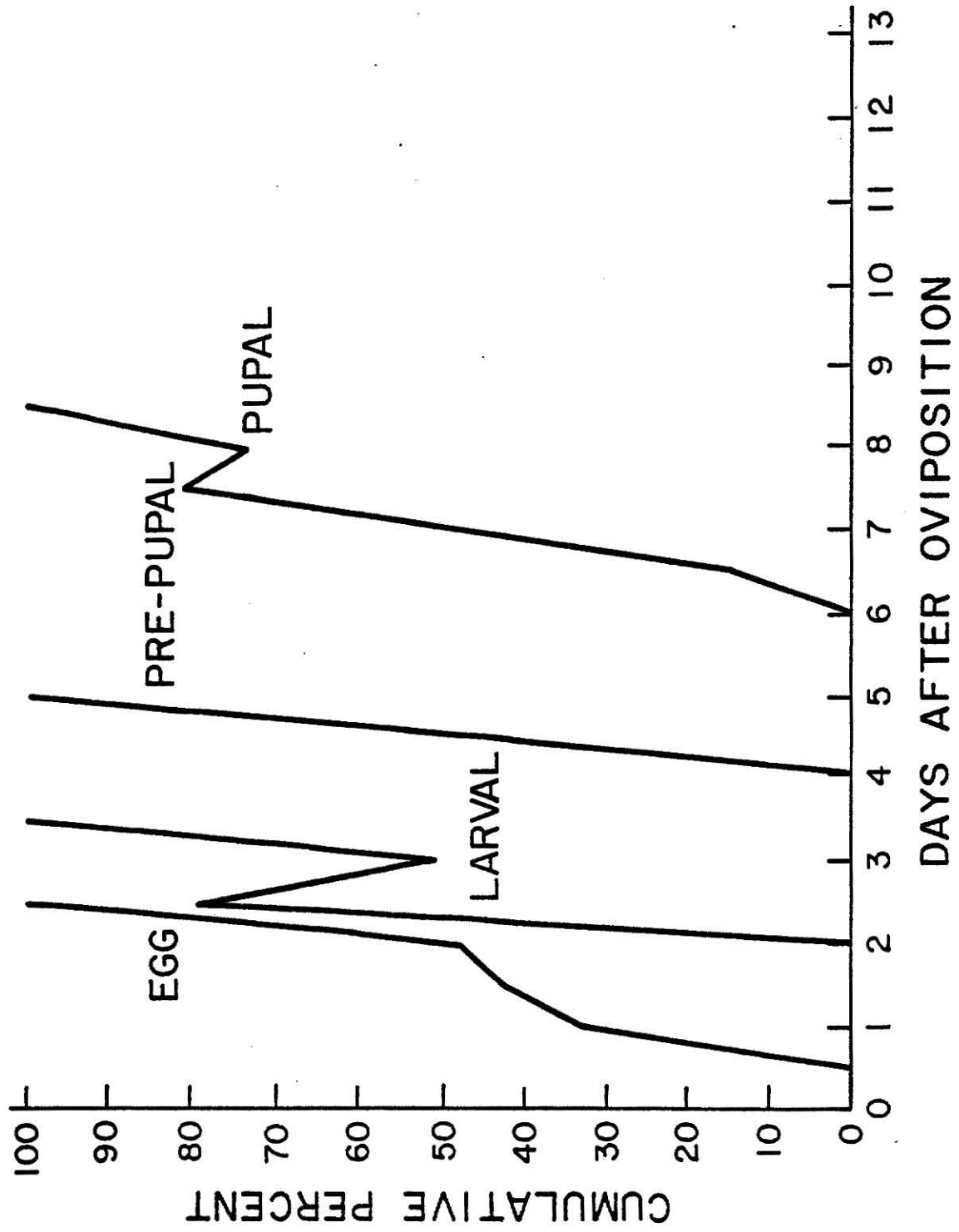


Figure 23. Observed percent completion of T. pretiosum life stages when reared at 30°C, 60% RH, and 12 h photophase.

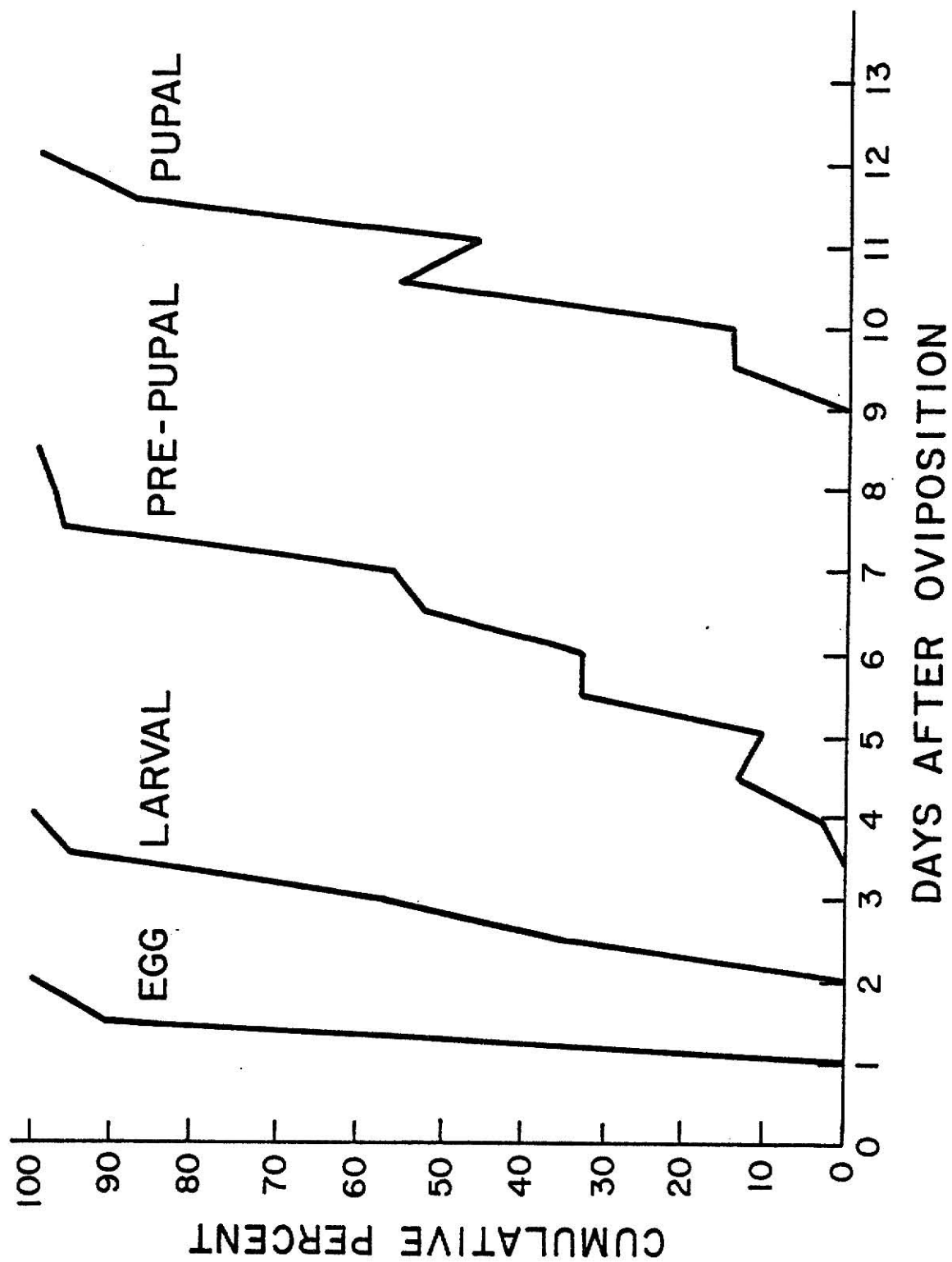
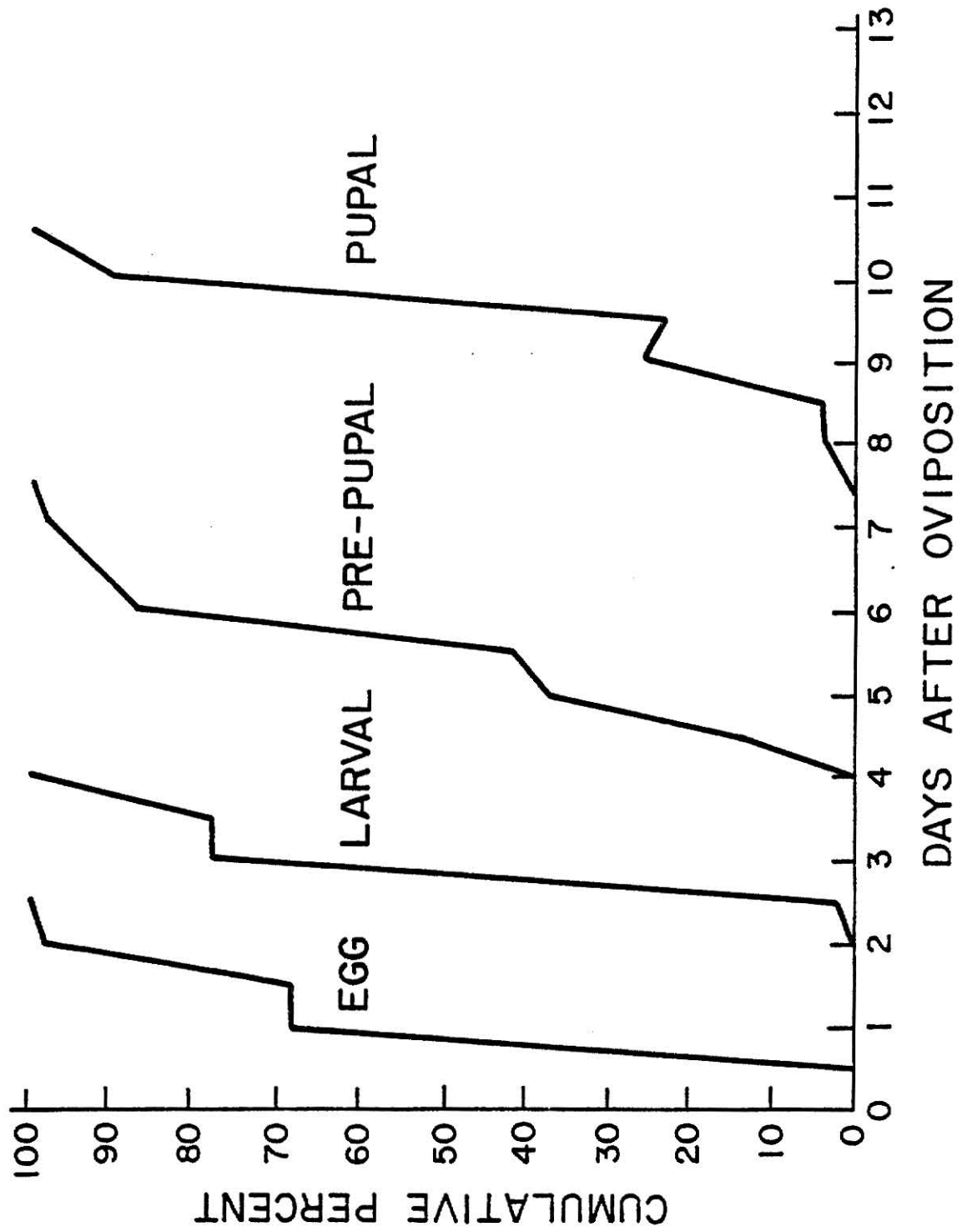


Figure 24. Observed percent completion of T. pretiosum life stages when reared at 30°C, 60% RH, and 16 h photophase.



APPENDIX III--Pearson's Correlation Coefficients.

VARIABLES MEASURED

<u>Abbreviation</u>	<u>Name</u>
TEMP	Temperature
PVOL	Parasite Volume (length x width ²)
SEX	Sex
LONG	Longevity
FE	Fecundity
PPH	Parasites Per Host
HVOL	Host Volume (length x width ²)
DT	Developmental Time

Table 16. Pearson's Correlation Coefficients between variables measured at constant temperature.

	TEMP	PVOL	SEX	LONG	FE	PPH	HVOL	DT
TEMP	1.000 0.000	0.251* 0.003	0.047 0.568	-0.610* 0.0001	-0.395* 0.003	0.127 0.127	-0.127 0.125	-0.859* 0.0001
PVOL		1.000 0.000	0.337 0.0001	-0.111 0.197	0.108 0.441	-0.261* 0.002	-0.051 0.548	-0.136 0.106
SEX			1.000 0.000	-0.023 0.790	0.000 1.000	0.022 0.794	-0.019 0.815	-0.061 0.465
LONG				1.000 0.000	0.247 0.078	-0.155 0.069	-0.125 0.143	0.730* 0.0001
FE					1.000 0.000	-0.253 0.068	0.149 0.288	0.234 0.091
PPH						1.000 0.000	0.279* 0.0007	-0.256* 0.0018
HVOL							1.000 0.000	-0.082 0.323
DT								1.000 0.000

*The relationship was significant at $P < 0.01$ level of significance.

Table 17. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 17°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	-0.190 0.364	-0.360 0.091	-----	-0.517* 0.008	0.266 0.199	0.593* 0.002
SEX		1.000 0.000	0.078 0.719	-----	0.299 0.122	0.219 0.263	-0.249 0.201
LONG			1.000 0.000	-----	0.609* 0.002	0.298 0.157	-0.891* 0.0001
FE				-----	-----	-----	-----
PPH					1.000 0.000	-0.136 0.491	-0.524* 0.004
HVOL						1.000 0.000	-0.279 0.150
DT							1.000 0.000

* The relationship was significant at $P < 0.01$ level of significance.

Table 18. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 20°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.212 0.343	0.335 0.127	0.445 0.170	-0.346 0.114	0.029 0.898	-0.178 0.429
SEX		1.000 0.000	0.406 0.0061	0.000 1.000	-0.056 0.805	-0.300 0.175	0.061 0.786
LONG			1.000 0.000	0.033 0.923	-0.061 0.789	-0.659* 0.0008	-0.080 0.724
FE				1.000 0.000	-0.555 0.076	-0.120 0.725	-0.172 0.613
PPH					1.000 0.000	0.040 0.858	-0.554* 0.007
HVOL						1.000 0.000	-0.034 0.880
DT							1.000 0.000

* The relationship was significant at $P < 0.01$ level of significance.

Table 19. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 22°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.286 0.132	0.528* 0.006	0.774 0.014	-0.515* 0.004	0.256 0.180	0.055 0.776
SEX		1.000 0.000	0.036 0.860	0.000 1.000	0.041 0.834	-0.226 0.240	-0.121 0.531
LONG			1.000 0.000	0.710 0.032	-0.461 0.018	0.016 0.938	-0.027 0.894
FE				1.000 0.000	-0.375 0.321	0.424 0.255	-0.290 0.450
PPH					1.000 0.000	-0.304 0.109	0.183 0.343
HVOL						1.000 0.000	-0.325 0.085
DT							1.000 0.000

* The relationship was significant at $P < 0.01$ level of significance.

Table 20. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 25°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.623* 0.0001	0.141 0.443	-0.050 0.853	-0.218 0.231	0.055 0.765	0.062 0.735
SEX		1.000 0.000	0.319 0.075	-----	-0.018 0.922	0.133 0.467	0.029 0.875
LONG			1.000 0.000	0.478 0.061	-0.408 0.020	-0.459 0.0082	0.052 0.777
FE				1.000 0.000	-0.241 0.368	-0.394 0.131	0.285 0.285
PPH					1.000 0.000	0.680* 0.0001	-0.274 0.129
HVOL						1.000 0.000	-0.132 0.471
DT							1.000 0.000

* The relationship was significant at $P < 0.01$ level of significance.

Table 21. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 30°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.473 0.020	-0.109 0.611	0.752* 0.003	-0.350 0.094	0.017 0.937	-0.088 0.683
SEX		1.000 0.000	0.232 0.265	-----	-0.143 0.485	0.192 0.348	-0.034 0.871
LONG			1.000 0.000	-0.139 0.650	-0.371 0.068	-0.221 0.288	-0.294 0.155
FE				1.000 0.000	-0.379 0.202	0.125 0.684	-0.325 0.279
PPH					1.000 0.000	0.082 0.691	0.393 0.047
HVOL						1.000 0.000	0.634* 0.0005
DT							1.000 0.000

*The relationship was significant at $P < 0.01$ level of significance.

Table 22. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 35°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.540 0.087	-0.823* 0.002	---	-0.312 0.414	-0.459 0.155	---
SEX		1.000 0.000	-0.235 0.486	---	-0.395 0.292	-0.474 0.141	---
LONG			1.000 0.000	---	0.534 0.138	0.642 0.033	---
FE				---	---	---	---
PPH					1.000 0.000	0.903* 0.0008	---
HVOL						1.000 0.000	---
DT							---

* The relationship was significant at $P < 0.01$ level of significance.

Table 23. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 28°C-32°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.472* 0.006	0.139 0.457	0.474 0.054	-0.127 0.482	0.127 0.487	-0.272 0.125
SEX		1.000 0.000	0.174 0.332	-----	-0.108 0.539	0.057 0.751	-0.100 0.567
LONG			1.000 0.000	-0.111 0.671	-0.099 0.583	-0.194 0.289	0.431 0.012
FE				1.000 0.000	-0.065 0.805	0.085 0.756	-0.430 0.085
PPH					1.000 0.000	0.089 0.615	-0.169 0.332
HVOL						1.000 0.000	0.145 0.414
DT							1.000 0.000

* The relationship was significant at $P < 0.01$ level of significance.

Table 25. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 22°C-38°C, 60% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.512 0.018	-0.340 0.234	-0.242 0.426	-0.024 0.919	-0.078 0.738	-0.112 0.628
SEX		1.000 0.000	0.255 0.379	-----	0.210 0.360	0.025 0.915	0.206 0.370
LONG			1.000 0.000	0.450 0.192	0.567 0.034	-0.369 0.195	0.155 0.600
FE				1.000 0.000	0.634 0.020	-0.022 0.942	0.167 0.585
PPH					1.000 0.000	0.327 0.149	0.557* 0.009
HVOL						1.000 0.000	0.465 0.034
DT							1.000 0.000

* The relationship was significant at $P < 0.01$ level of significance.

Table 27. Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 30°C, 80% RH, and 14 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.619 0.001	0.254 0.232	0.708 0.010	-0.534 0.006	-0.078 0.710	-0.170 0.417
SEX		1.000 0.000	0.525 0.008	-----	-0.097 0.643	-0.222 0.287	-0.374 0.066
LONG			1.000 0.000	0.408 0.213	-0.154 0.474	-0.096 0.657	-0.651* 0.0006
FE				1.000 0.000	-0.801* 0.0017	-0.166 0.606	0.435 0.158
PPH					1.000 0.000	-0.133 0.526	-0.139 0.508
HVOL						1.000 0.000	0.201 0.335
DT							1.000 0.000

*The relationship was significant at $P < 0.01$ level of significance.

Table 28, Pearson's Correlation Coefficients between variables measured when T. pretiosum was reared at 30°C, 60% RH, and 12 h photophase.

	PVOL	SEX	LONG	FE	PPH	HVOL	DT
PVOL	1.000 0.000	0.416 0.097	-0.270 0.373	-0.351 0.440	0.095 0.724	-0.025 0.924	-0.054 0.326
SEX		1.000 0.000	0.065 0.832	0.000 1.000	-0.058 0.825	0.288 0.263	-0.105 0.688
LONG			1.000 0.000	0.000 1.000	-0.455 0.102	0.181 0.536	0.469 0.091
FE				1.000 0.000	-0.032 0.946	-0.664 0.104	-0.304 0.508
PPH					1.000 0.000	-0.479 0.044	-0.251 0.315
HVOL						1.000 0.000	0.578 0.012
DT							1.000 0.000

APPENDIX IV--Parasites per host egg frequency distributions.

Figure 25. Frequency distribution of parasites per host from field parasitized southwestern corn borer eggs.

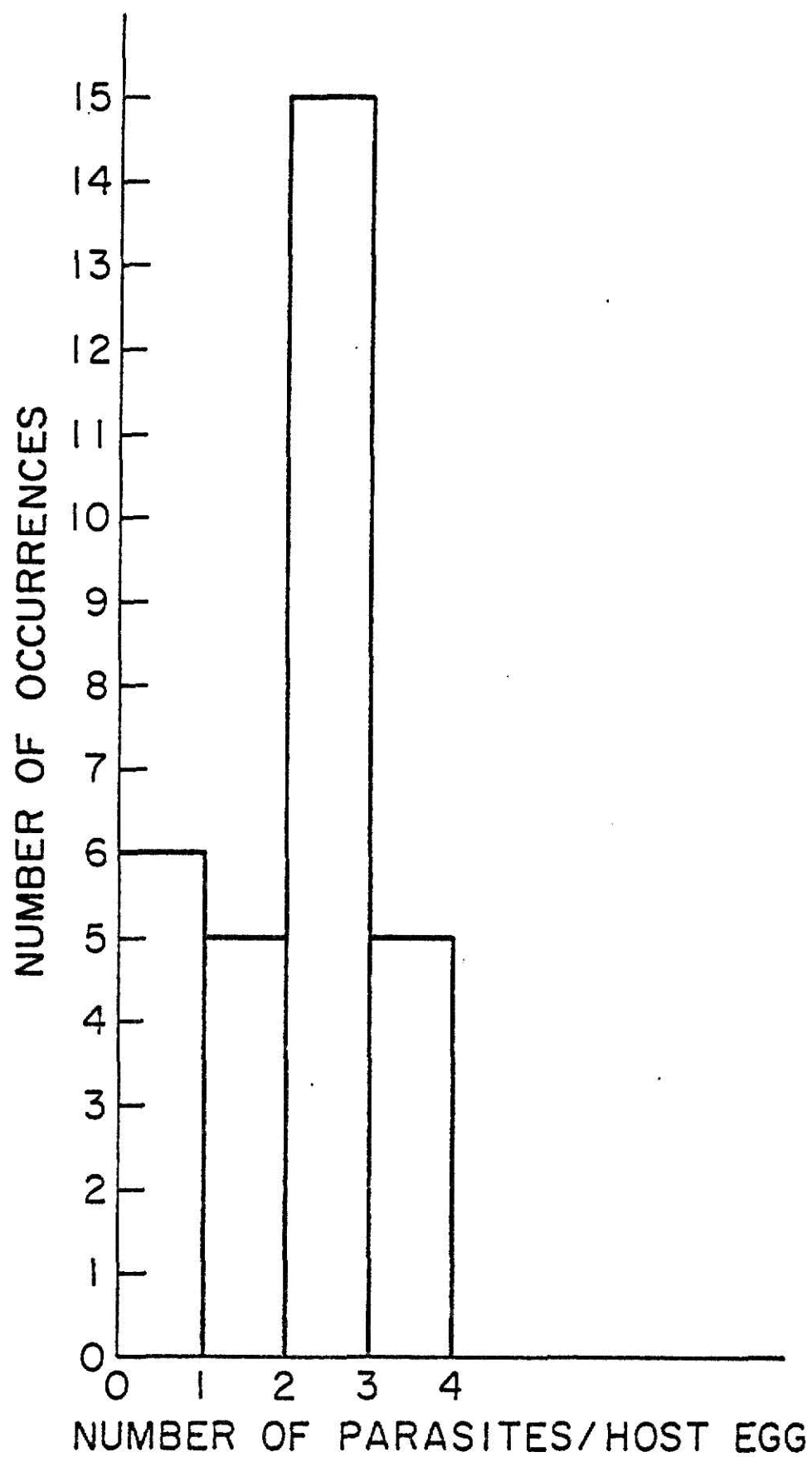


Figure 26. Frequency distribution of parasites per host egg for all laboratory studies.

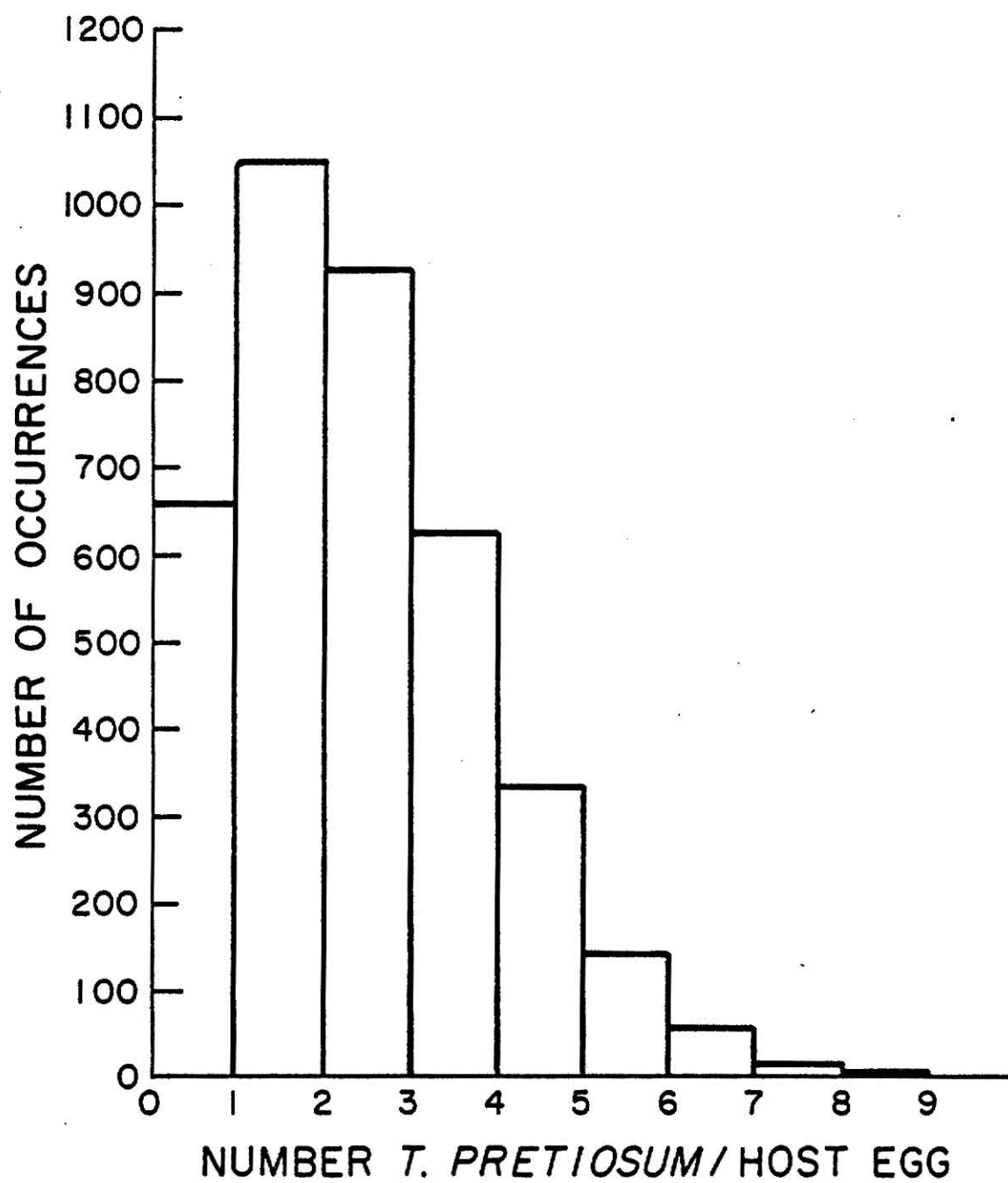


Figure 27. Frequency distribution of parasites per host egg at 17°C, 60% RH, and 14 h photophase.

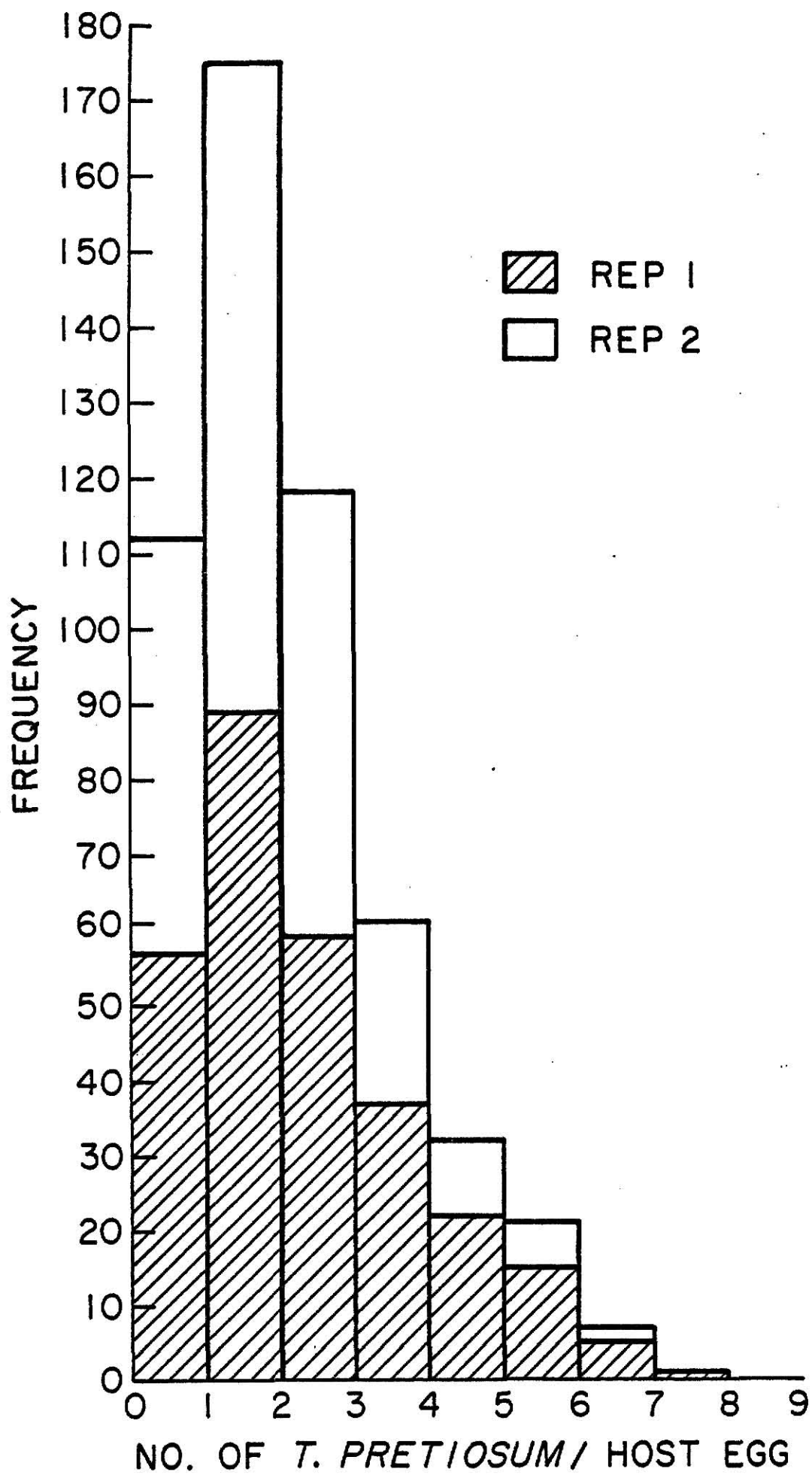


Figure 28. Frequency distribution of parasites per host egg at 20°C, 60% RH, and 14 h photophase.

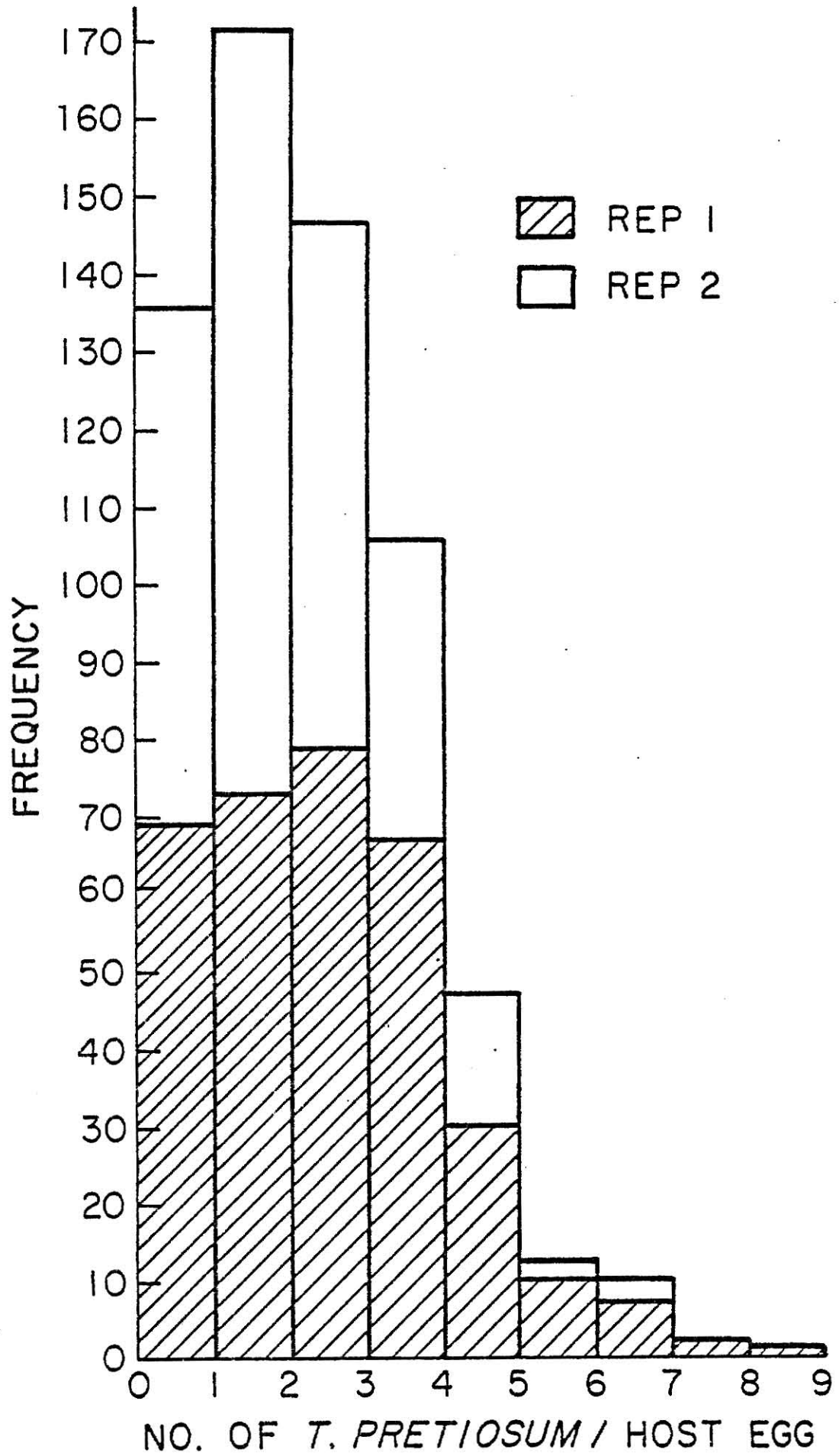


Figure 29. Frequency distribution of parasites per host egg at 22°C, 60% RH, and 14 h photophase.

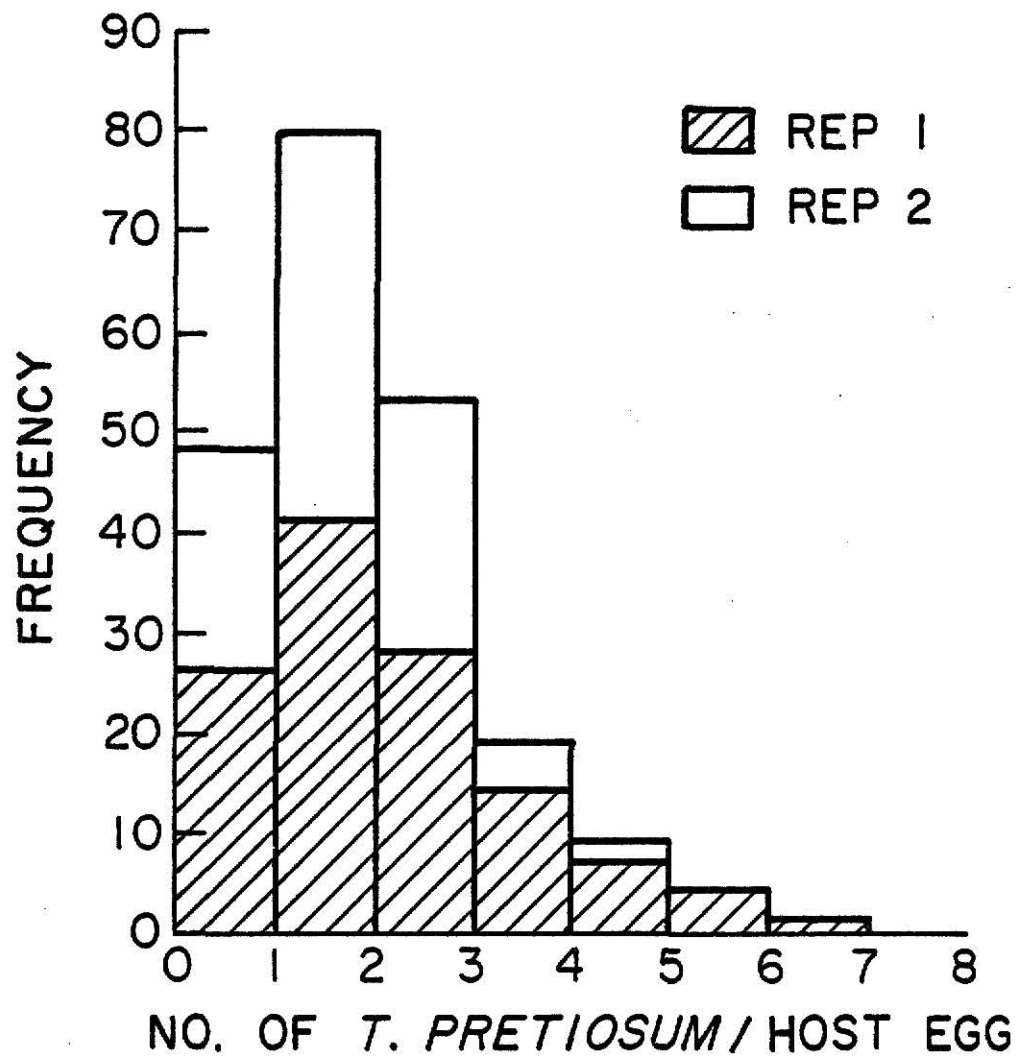


Figure 30. Frequency distribution of parasites per host egg at 25°C, 60% RH, and 14 h photophase.

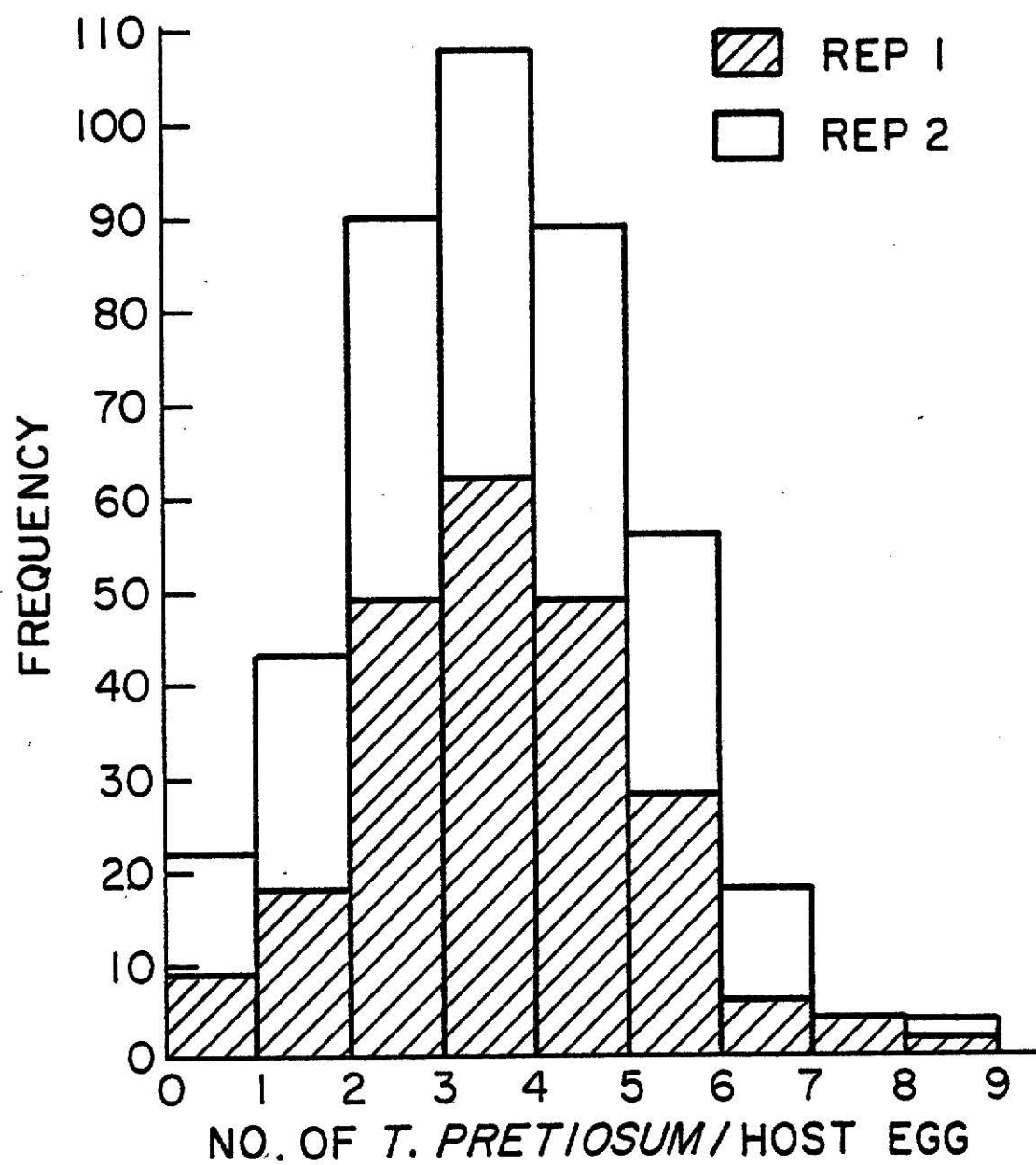


Figure 31. Frequency distribution of parasites per host egg at 30°C, 60% RH, and 14 h photophase.

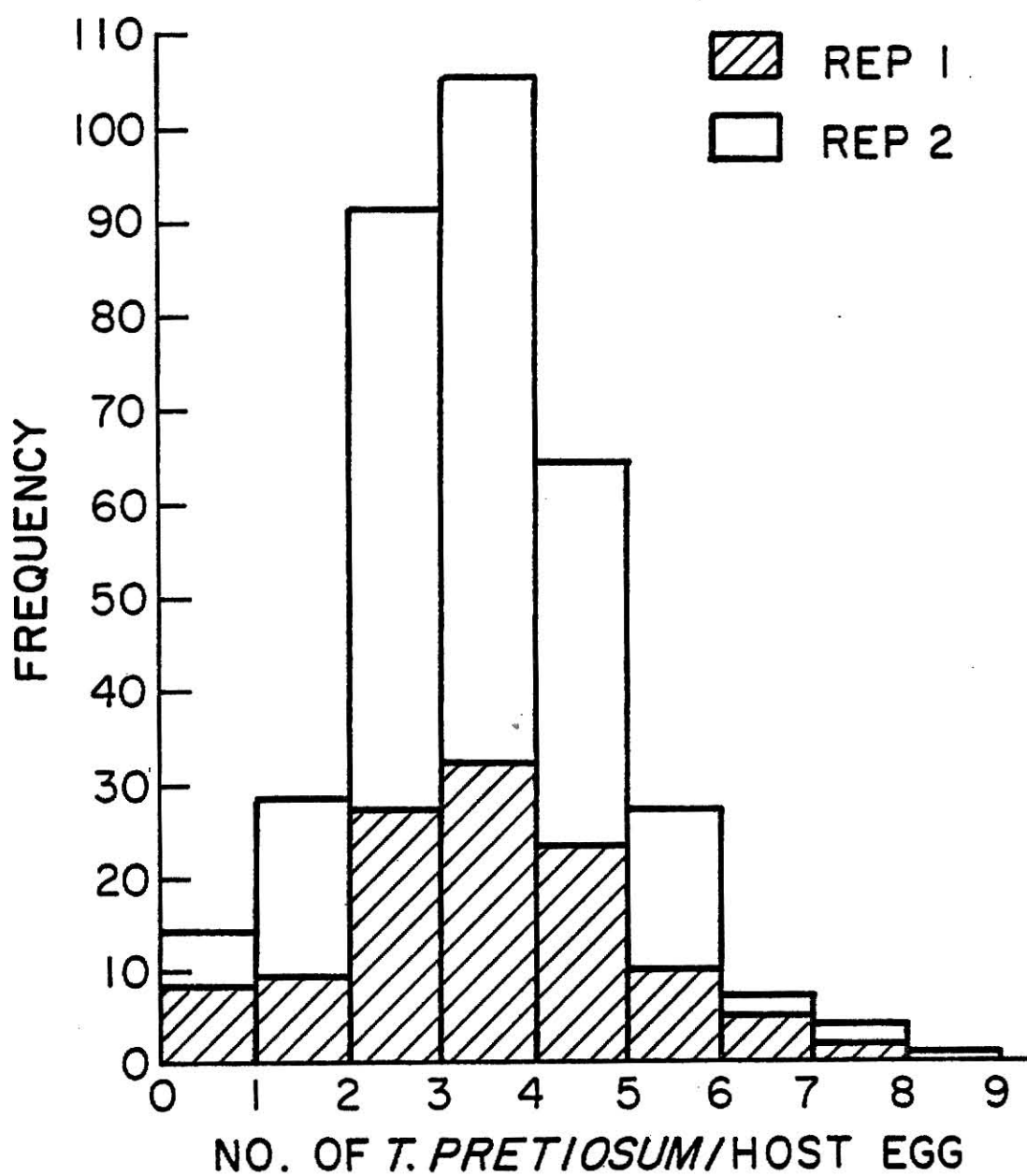


Figure 32. Frequency distribution of parasites per host egg at 35°C, 60% RH, and 14 h photophase.

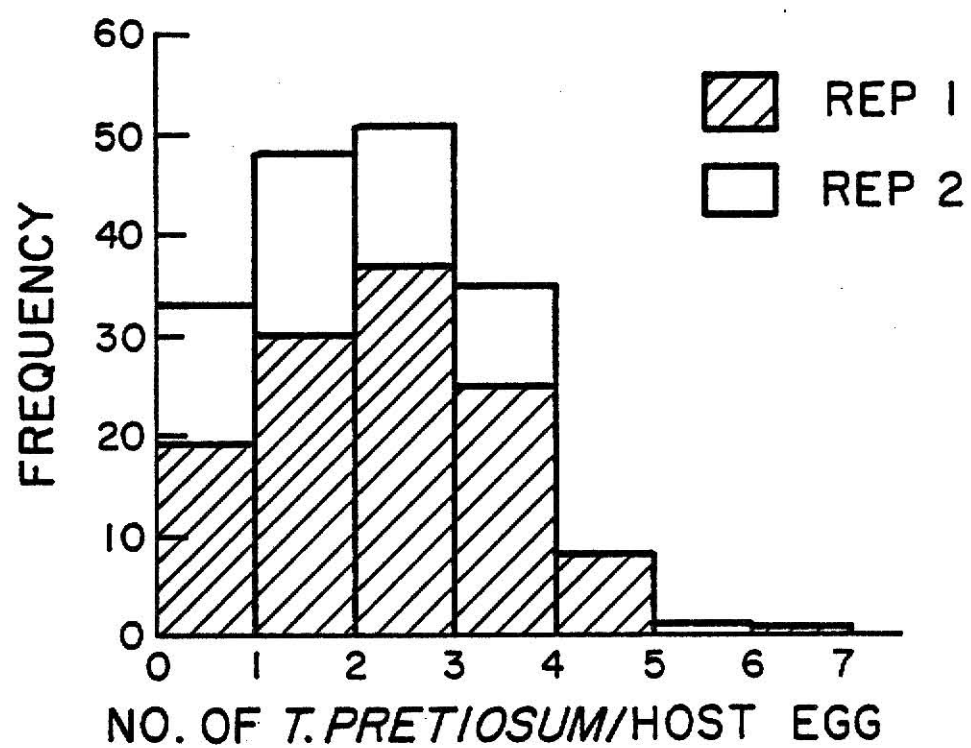


Figure 33. Frequency distribution of parasites per host egg at 28°C-32°C, 60% RH, and 14 h photophase.

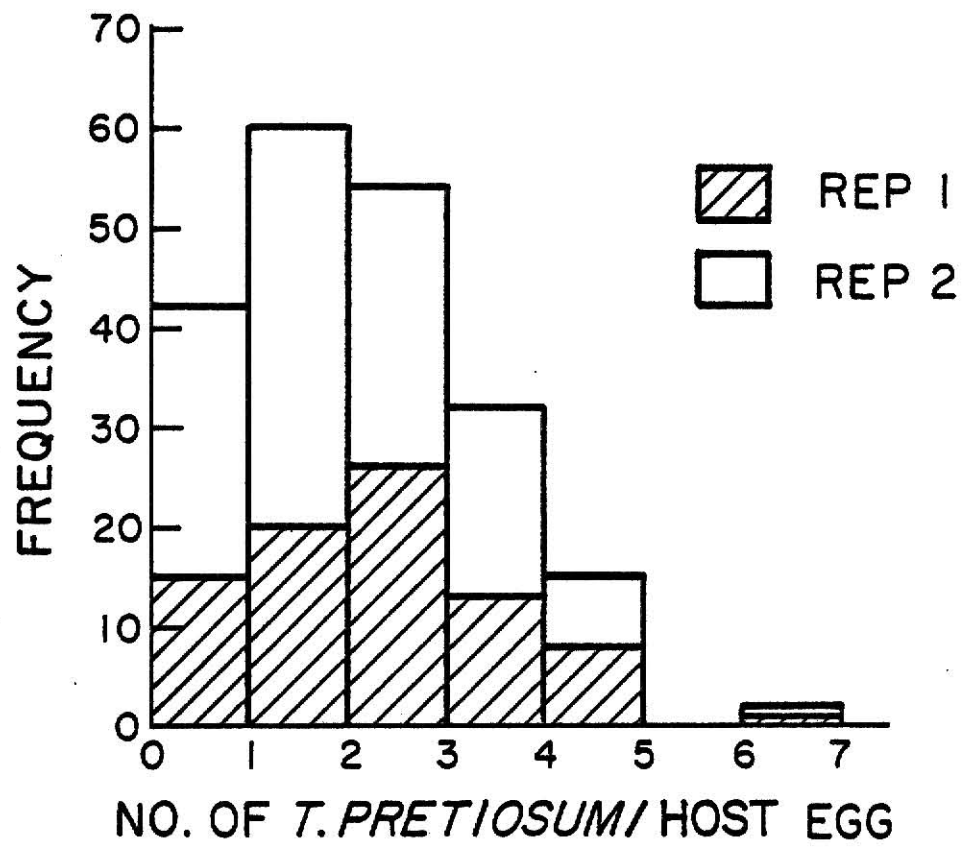


Figure 34. Frequency distribution of parasites per host egg at 26°C-34°C, 60% RH, and 14 h photophase.

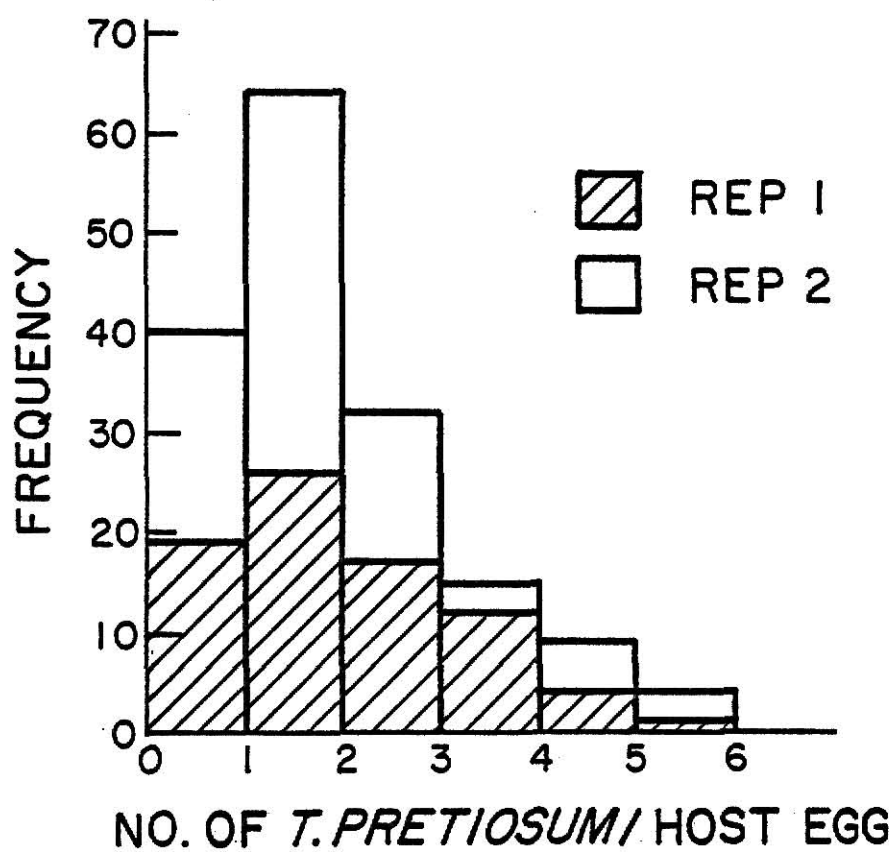


Figure 35. Frequency distribution of parasites per host egg at 22°C-38°C, 60% RH, and 14 h photophase.

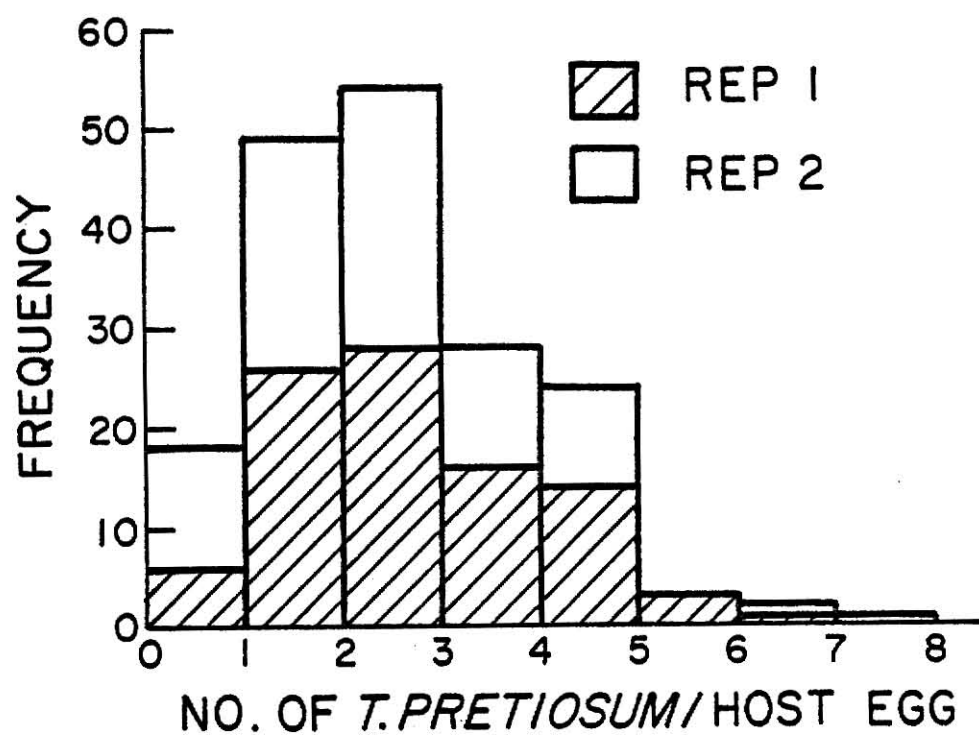


Figure 36. Frequency distribution of parasites per host egg at 30°C, 20% RH, and 14 h photophase.

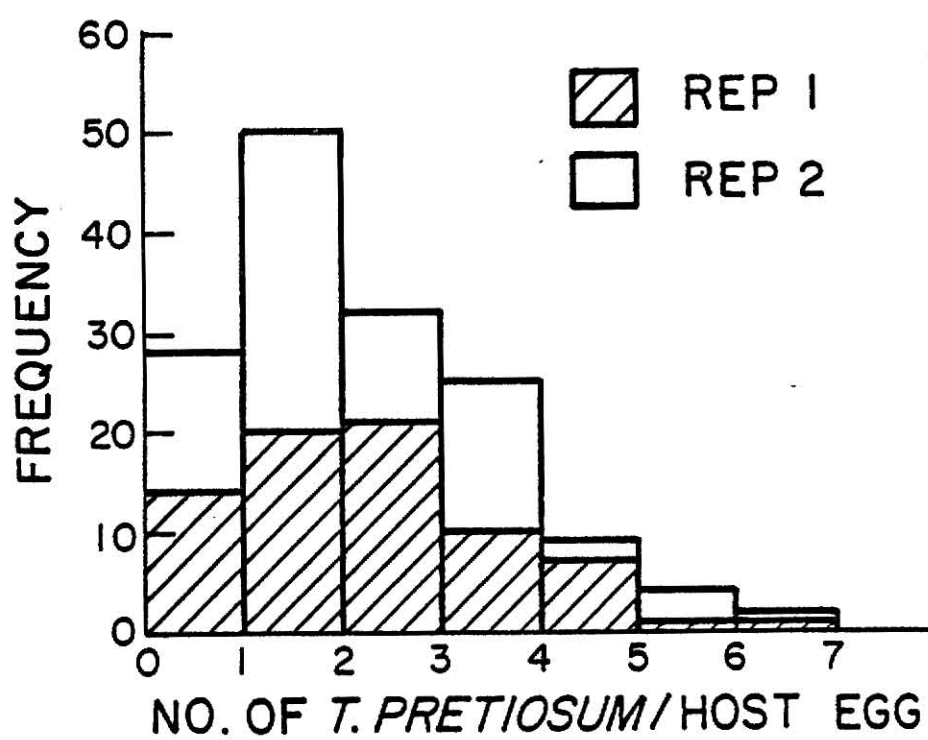


Figure 37. Frequency distribution of parasites per host egg at 30°C, 80% RH, and 14 h photophase.

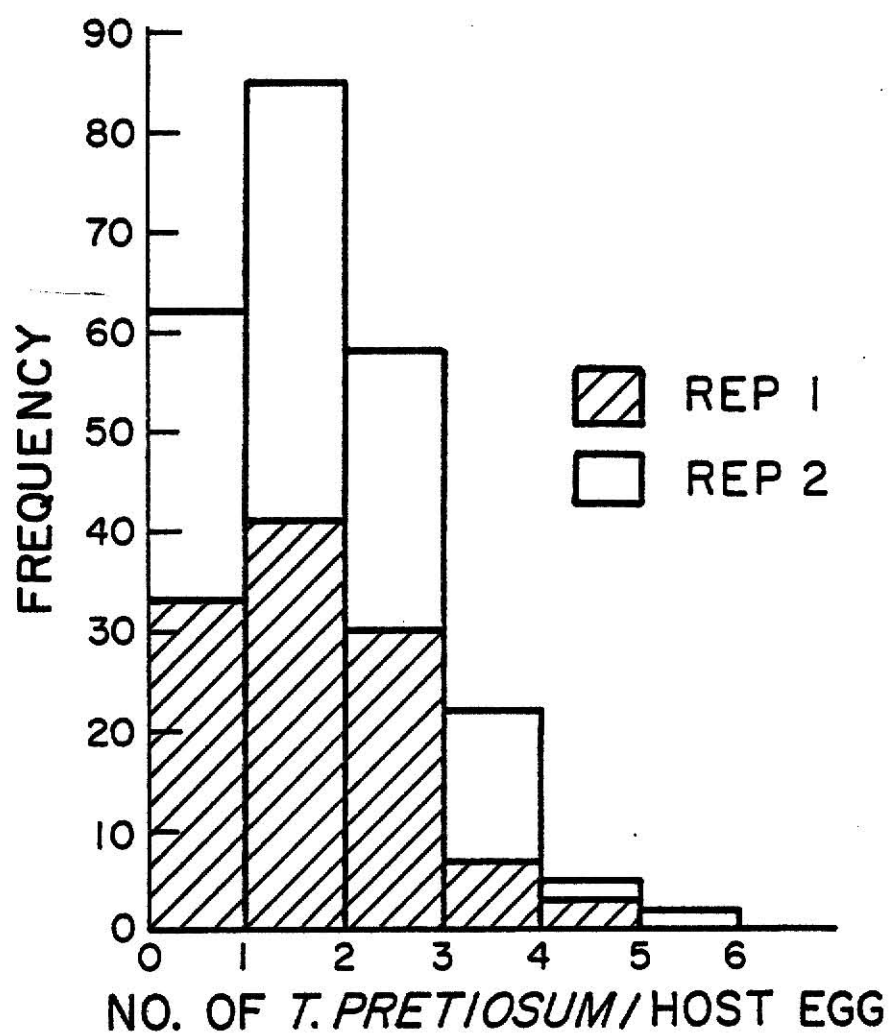


Figure 38. Frequency distribution of parasites per host egg at 30°C, 60% RH, and 12 h photophase.

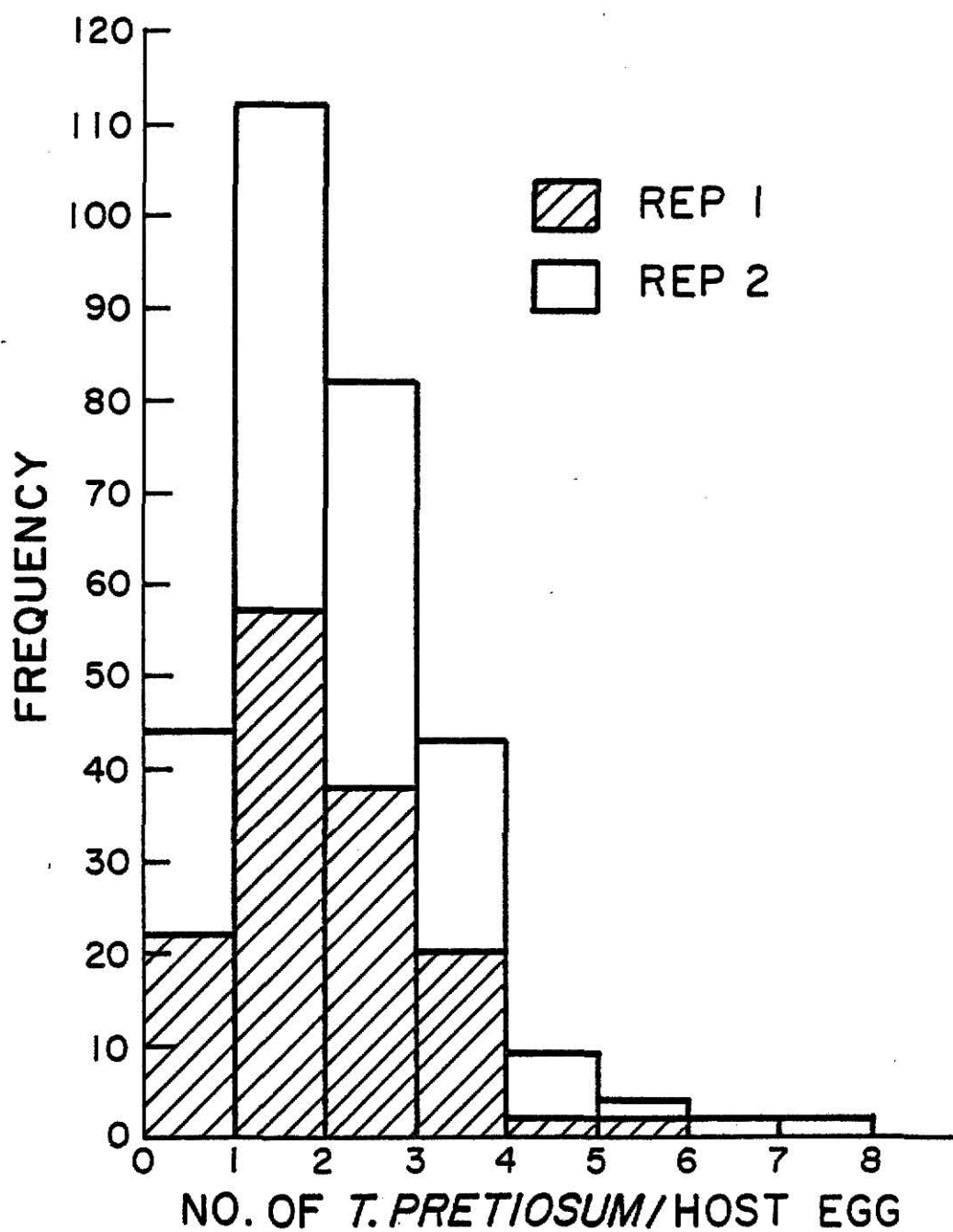
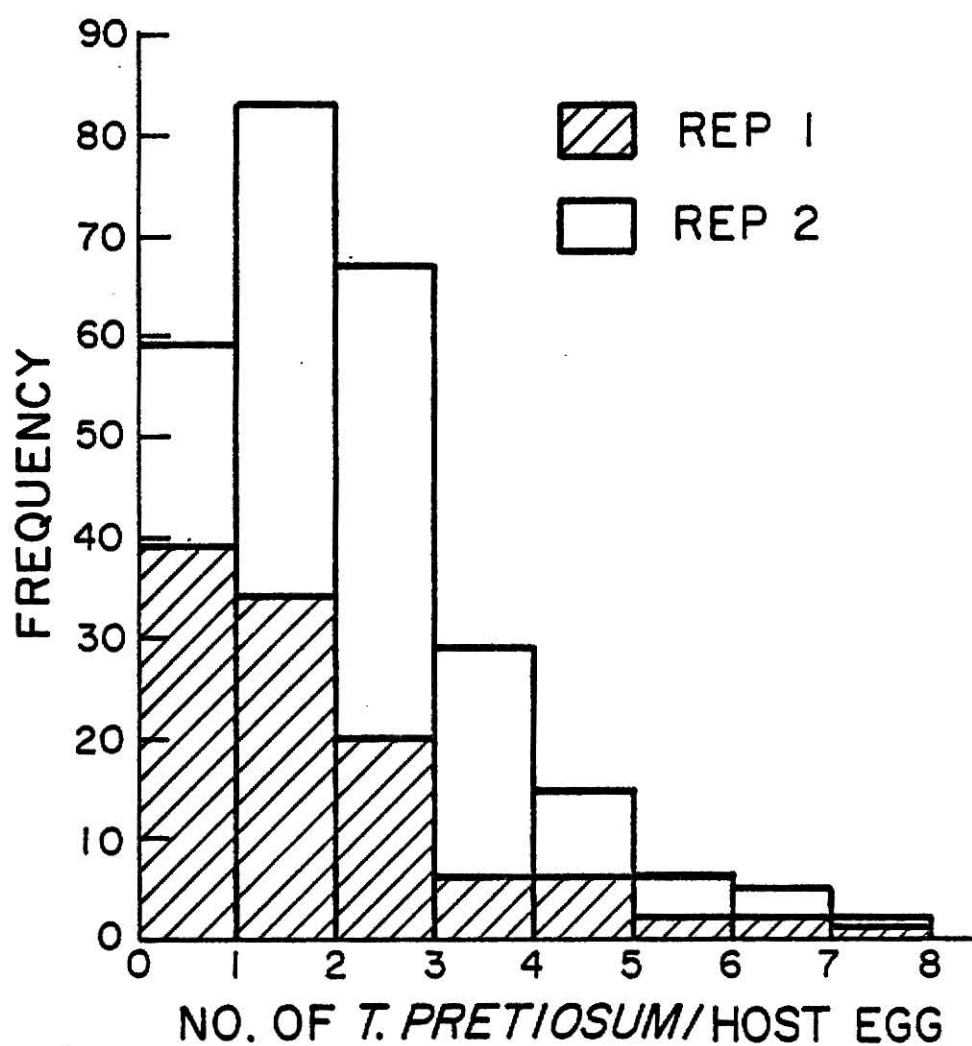


Figure 39. Frequency distribution of parasites per host egg at 30°C, 60% RH, and 16 h photophase.



APPENDIX V--Growth chamber fluctuation regimes.

Figure 40. Daily temperature fluctuation for 28°C-32°C.

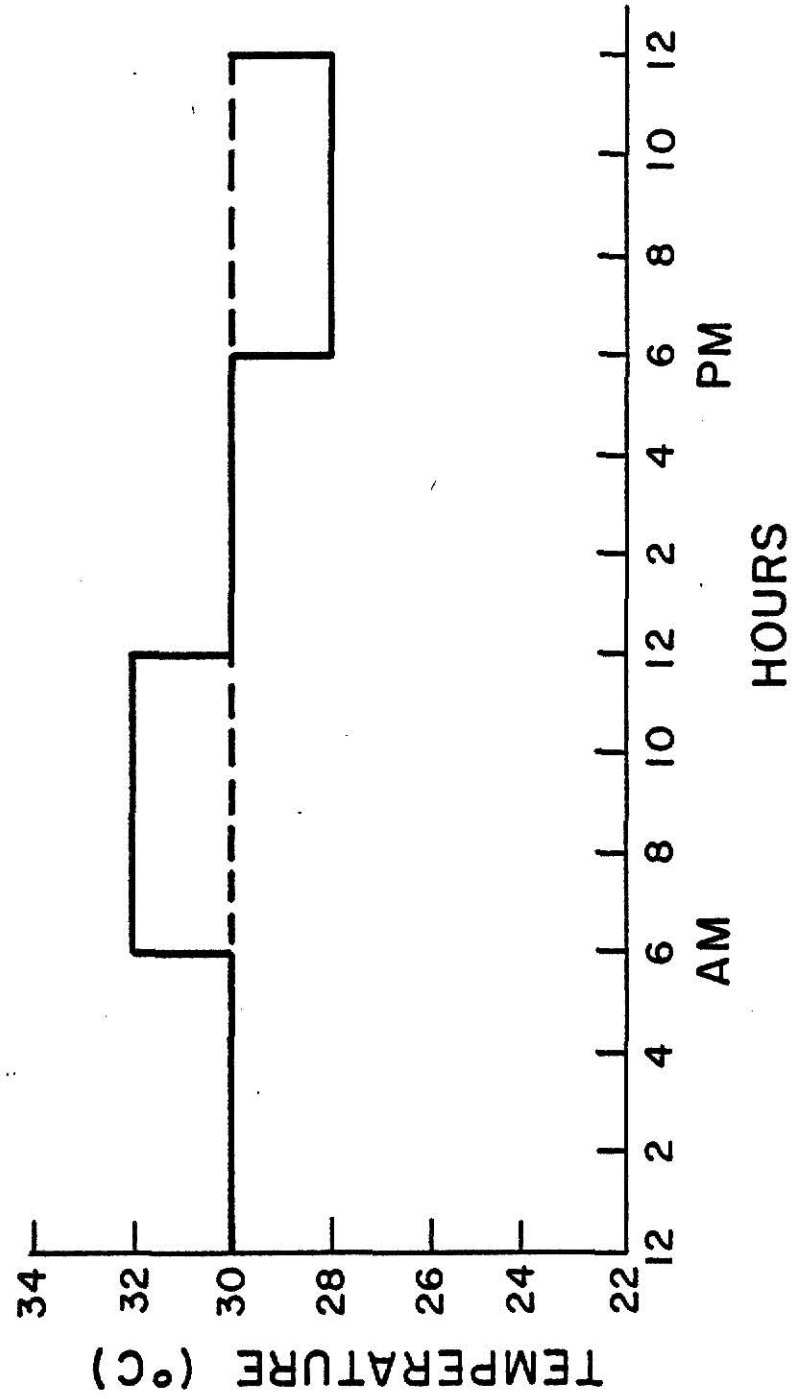


Figure 41. Daily temperature fluctuation for 26°C-34°C.

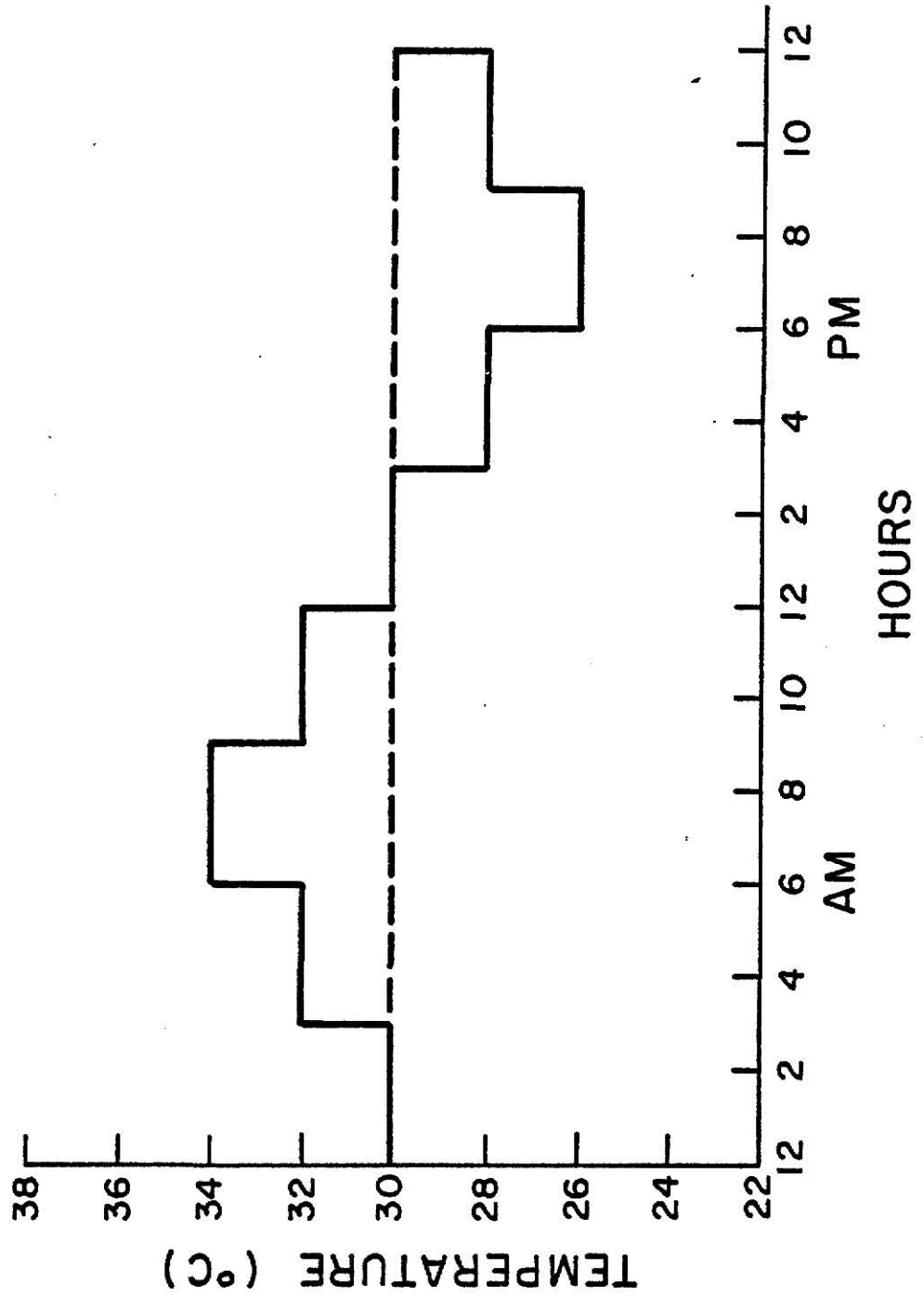
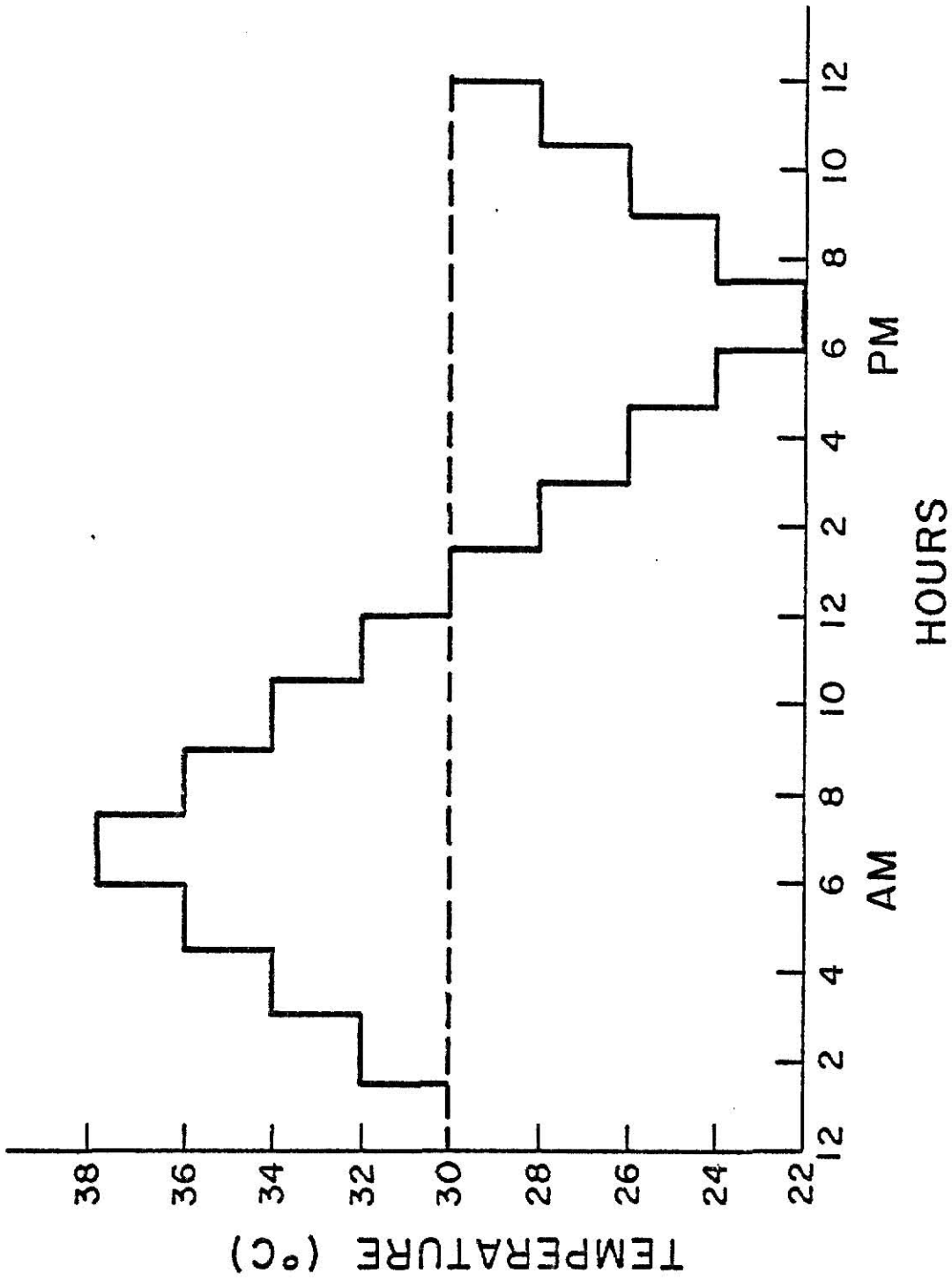


Figure 42. Daily temperature fluctuation for 22°C-38°C.



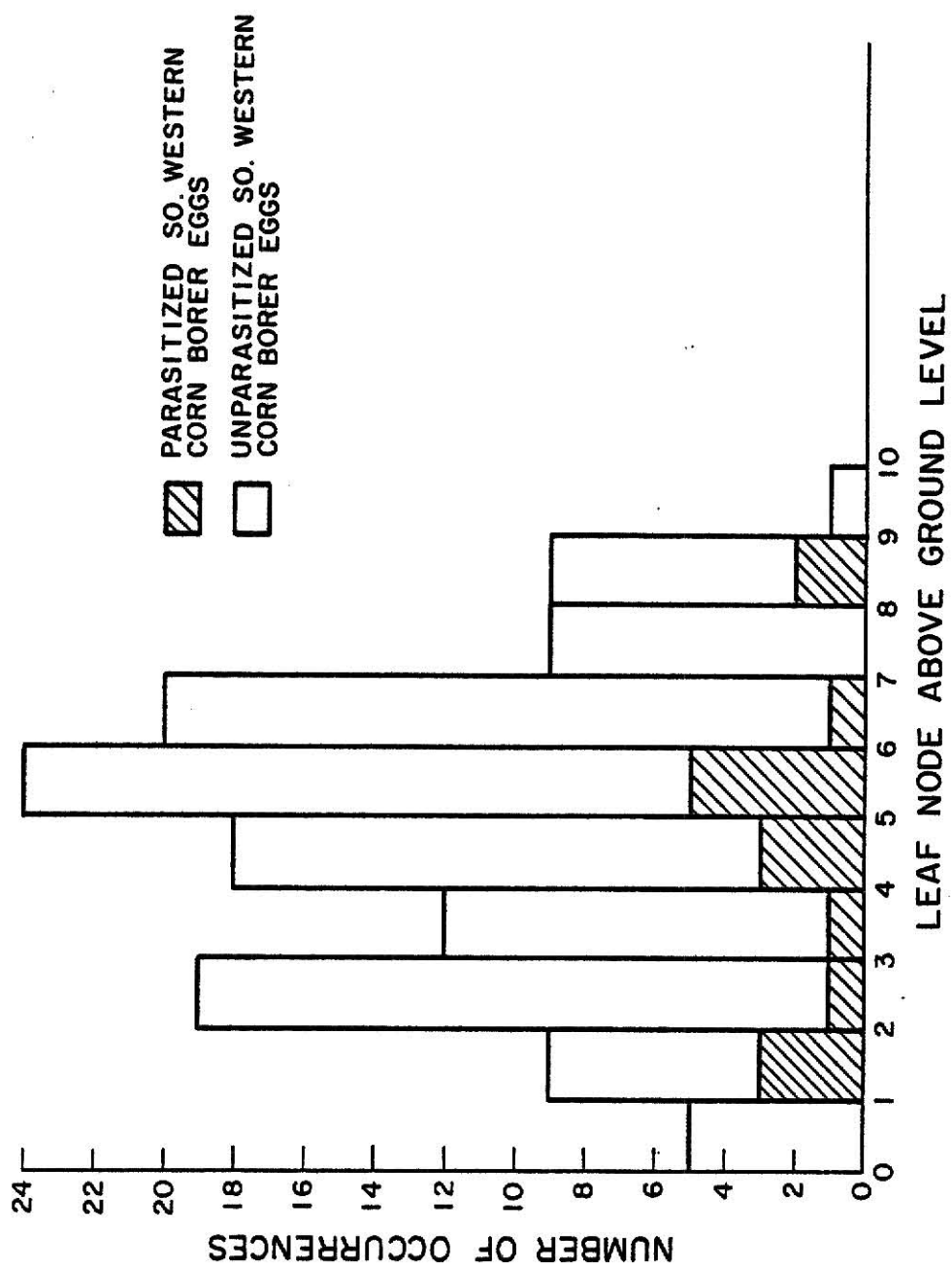
APPENDIX VI--Calculations to predict T. pretiosum Riley developmental time under a 22°C-38°C fluctuating temperature regime.

Table 30. Calculations to predict T. pretiosum Riley developmental time from oviposition to 50% adult emergence under a 22°C-38°C fluctuating temperature regime.

Temperature (C°)	hr/day	Proportion of day	PDT ^a (days)	1/days	1/dev. ^b contribution	DC ^c
22	1.5	0.063	14.83	0.067	0.0042	
24	3.0	0.125	11.40	0.088	0.110	
26	3.0	0.125	9.01	0.111	0.0139	
28	3.0	0.125	7.57	0.132	0.0165	
30	3.0	0.125	7.12	0.140	0.0175	
32	3.0	0.125	7.65	0.131	0.0164	
34	3.0	0.125	9.17	0.109	0.0136	
36	3.0	0.125	11.67	0.086	0.0108	
38	1.5	0.063	15.15	0.066	0.0042	
Total					0.108	9.25

APPENDIX VII--Height above ground level of parasitized and
unparasitized southwestern corn borer eggs at
St. John, Kansas, during 1979.

Figure 43. Height above ground level of parasitized and unparasitized southwestern corn borer eggs at St. John, Kansas, during 1979.



APPENDIX VIII--Maximum, minimum, and average daily temperatures
during 1979 and 1980.

Table 31. Maximum, minimum, and average daily temperatures during 1979
at Sandyland Experiment Field, St. John, Kansas.

DATE	MAXIMUM	MINIMUM	AVERAGE
July 26	87	64	75.5
27	87	69	78.0
28	89	64	76.5
29	95	69	82.0
30	96	67	81.5
31	90	65	77.5
Aug. 1	80	65	72.5
2	89	66	77.5
3	91	63	77.0
4	93	67	80.0
5	97	66	81.5
6	95	72	83.5
7	97	74	85.5
8	99	71	85.0
9	97	68	82.5
10	97	69	83.0
11	80	52	66.0
12	78	56	67.0
13	86	60	78.0
14	93	57	75.0
15	60	49	54.5
16	63	49	56.0
17	90	61	75.5
18	90	62	76.0
19	89	58	73.5
20	88	55	71.5
21	86	54	70.0
22	89	61	75.0

Table 32. Maximum, minimum, and average daily temperatures during 1980
at Sandyland Experiment Field, St. John, Kansas.

DATE	MAXIMUM	MINIMUM	AVERAGE
July 26	89	65	72.0
27	94	62	78.0
28	104	68	86.0
29	106	72	89.0
30	105	77	91.0
31	100	75	87.5
Aug. 1	109	73	91.0
2	102	78	90.0
3	104	70	87.0
4	93	72	82.5
5	102	67	84.5
6	99	67	83.0
7	100	74	87.0
8	100	74	87.0
9	100	76	88.0
10	103	76	89.5
11	91	69	80.0
12	99	67	83.0
13	100	74	87.0
14	80	68	74.0
15	84	68	76.0
16	91	66	78.5
17	87	67	77.0
18	95	68	81.5
19	96	74	85.0
20	88	66	77.0
21	82	59	70.5
22	86	64	75.0

APPENDIX IX--Predicted percent T. pretiosum parasitism of SWCB
eggs based on model assumptions.

Table 33. Predicted percent T. pretiosum parasitism of SWCB eggs
for possible variable and parameter combinations using
the theoretical model.

Immature Mortality (%)	Probability of Locating a Host (%)	Initial Adult Parasite Population (#/Acre)	Seasonal SWCB Egg Population (#/Acre)	Percent Parasitism
25	25	50	48,000	0.49
25	25	50	96,000	0.24
25	25	50	192,000	0.12
25	25	100	48,000	0.98
25	25	100	96,000	0.49
25	25	100	192,000	0.24
25	25	500	48,000	4.91
25	25	500	96,000	2.45
25	25	500	192,000	1.23
25	25	1000	48,000	8.54
25	25	1000	96,000	4.91
25	25	1000	192,000	2.45
25	50	50	48,000	2.84
25	50	50	96,000	1.42
25	50	50	192,000	0.71
25	50	100	48,000	5.69
25	50	100	96,000	2.84
25	50	100	192,000	1.42
25	50	500	48,000	24.69
25	50	500	96,000	14.22
25	50	500	192,000	7.11
25	50	1000	48,000	23.27
25	50	1000	96,000	24.69
25	50	1000	192,000	14.22

Immature Mortality (%)	Probability of Locating a Host (%)	Initial Adult Parasite Population (#/Acre)	Seasonal SWCB Egg Population (#/Acre)	Percent Parasitism
25	75	50	48,000	8.61
25	75	50	96,000	4.31
25	75	50	192,000	2.15
25	75	100	48,000	17.22
25	75	100	96,000	8.61
25	75	100	192,000	4.31
25	75	500	48,000	42.68
25	75	500	96,000	42.18
25	75	500	192,000	21.53
25	75	1000	48,000	54.17
25	75	1000	96,000	42.68
25	75	1000	192,000	42.18
50	25	50	48,000	0.30
50	25	50	96,000	0.15
50	25	50	192,000	0.07
50	25	100	48,000	0.59
50	25	100	96,000	0.30
50	25	100	192,000	0.15
50	25	500	48,000	2.95
50	25	500	96,000	1.47
50	25	500	192,000	0.74
50	25	1000	48,000	5.14
50	25	1000	96,000	2.95
50	25	1000	192,000	1.48
50	50	50	48,000	1.49
50	50	50	96,000	0.74
50	50	50	192,000	0.37
50	50	100	48,000	2.97
50	50	100	96,000	1.49
50	50	100	192,000	0.74
50	50	500	48,000	12.93
50	50	500	96,000	7.44
50	50	500	192,000	3.72

Immature Mortality (%)	Probability of Locating a Host (%)	Initial Adult Parasite Population (#/Acre)	Seasonal SWCB Egg Population (#/Acre)	Percent Parasitism
50	50	1000	48,000	12.20
50	50	1000	96,000	12.93
50	50	1000	192,000	7.44
50	75	50	48,000	4.27
50	75	50	96,000	2.13
50	75	50	192,000	1.07
50	75	100	48,000	8.53
50	75	100	96,000	4.27
50	75	100	192,000	2.13
50	75	500	48,000	21.15
50	75	500	96,000	20.90
50	75	500	192,000	10.67
50	75	1000	48,000	27.52
50	75	1000	96,000	21.15
50	75	1000	192,000	20.90
75	25	50	48,000	0.16
75	25	50	96,000	0.08
75	25	50	192,000	0.04
75	25	100	48,000	0.31
75	25	100	96,000	0.16
75	25	100	192,000	0.08
75	25	500	48,000	1.57
75	25	500	96,000	0.80
75	25	500	192,000	0.40
75	25	1000	48,000	2.74
75	25	1000	96,000	1.57
75	25	1000	192,000	0.79
75	50	50	48,000	0.59
75	50	50	96,000	0.30
75	50	50	192,000	0.15
75	50	100	48,000	1.18
75	50	100	96,000	0.59
75	50	100	192,000	0.30

Immature Mortality (%)	Probability of Locating a Host (%)	Initial Adult Parasite Population (#/Acre)	Seasonal SWCB Egg Population (#/Acre)	Percent Parasitism
75	50	500	48,000	5.14
75	50	500	96,000	2.95
75	50	500	192,000	1.48
75	50	1000	48,000	4.86
75	50	1000	96,000	5.14
75	50	1000	192,000	2.95
75	75	50	48,000	1.48
75	75	50	96,000	0.74
75	75	50	192,000	0.38
75	75	100	48,000	2.94
75	75	100	96,000	1.47
75	75	100	192,000	0.74
75	75	500	48,000	7.30
75	75	500	96,000	7.21
75	75	500	192,000	3.68
75	75	1000	48,000	9.58
75	75	1000	96,000	7.30
75	75	1000	192,000	7.21

THE IMPACT OF VARIOUS ENVIRONMENTAL FACTORS
ON Trichogramma pretiosum Riley BIOLOGY
WHEN REARED ON SOUTHWESTERN CORN BORER EGGS

by

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The effect of constant temperature, fluctuating temperature, relative humidity, and photophase on T. pretiosum Riley developmental time, longevity, fecundity, and sex ratio were investigated. Median developmental times of immature T. pretiosum life stages were determined for constant temperatures 17°C, 20°C, 22°C, 25°C, 30°C, and 35°C. Developmental time curves for all parasite life stages were described by second degree polynomial equations. Optimum development was predicted to be at 30°C for all life stages. However, optimum development probably falls between 25°C and 35°C. Longevity was approximately two days under constant temperatures with the exception of 17°C and 35°C (7.67 and 0.60 days, respectively). When reared under constant temperatures, fecundity was 18 ova/female below 25°C and 9 ova/female above 30°C. For all studies, sex ratio was affected by the number of parasites per host egg.

Four fluctuating regimes (30°C, 28°C-32°C, 26°C-34°C, and 22°C-38°C) were compared. Median developmental time was affected very little by fluctuating the temperature. Fecundity was not influenced by fluctuating temperatures. Male and female longevity were not significantly affected by fluctuating temperatures.

Relative humidities 20%, 60%, and 80% were investigated. Developmental time at 20% RH was approximately two days longer than at 60% RH and 80% RH. Adult female longevity was also significantly longer at 20% RH. However, fecundity was significantly greater at 80% RH.

Photophases of 12 h, 14 h, and 16 h were compared. Developmental time increased under 12 h and 16 h photophases. Female longevity was significantly longer under a 12 h photophase.

During 1978 and 1979, SWCB oviposition and Trichogramma parasitism were observed. Trichogramma parasitism appeared to follow the second generation SWCB oviposition period. Unparasitized SWCB egg masses averaged 2.05 eggs/mass and parasitized eggs averaged 2.93 eggs/mass. Field parasitized host eggs, on the average, contained 2.79 parasites/host egg, with a range of from one to four parasites per host egg. Parasitism of the naturally occurring SWCB egg population during 1979 was 12.25%, as compared to 7.26% for artificially infested eggs.

A theoretical model was developed to investigate the potential of T. pretiosum as a biological control agent of the SWCB. Parasitism under the best conditions defined by the model, without augmenting the population, was 50.7%. Augmenting the population resulted in variable levels of control. Based on model simulations, T. pretiosum probably completes two generations during the SWCB second generation oviposition period.