FACTORS INFLUENCING DEVELOPMENTAL RATES AND PARASITIZATION CAPABILITIES OF THE PENTATOMID EGG PARASITE, TELENOMUS UTAHENSIS ASHMEAD (HYMENOPTERA: SCELIONIDAE)

by

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STATEMENT BY AUTHOR

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May 11, 1962
Date

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ABSTRACT

Developmental rates and parasitization capabilities of the pentatomid egg parasite, Telenomus utahensis Ashmead, were studied in relation to host age at six constant temperatures (59°, 68°, 77°, 81°, 86°, and 95°F.).

At 68°F. and above, the rate of parasite development in eggs of the two hosts studied, Chlorochroa uhleri Stål and C. sayi Stål (Hemiptera: Pentatomidae), increased as the temperature increased, but below 68°F. development usually did not occur. Developmental rates were similar in the two hosts and did not change when the age of the host egg varied from less than one to four days at the time of parasite oviposition. Development occurred at 81° and 77°F. in C. uhleri eggs that had completed one-half their incubation period. The parasite required twice the normal C. uhleri incubation period for development.

Parasitism was highest (70-80%) in less-than-one-day-old eggs and generally decreased as host age increased. Per cent parasitism was approximately 8% higher in the various-aged C. uhleri eggs at all temperatures. The maximum parasitization recorded for an individual female

in this study was 66 host eggs. Higher percentages of females than males were usually found in parasite F_1 progeny reared in the laboratory.

INTRODUCTION

The egg parasite, Telenomus utahensis Ashmead (= Hadronotus mesillae Cockerell, = T. ashmeadi Morrill), is an important natural enemy of several pentatomids that attack various crops in Arizona. It is found also in California, Colorado, Idaho, New Mexico, Texas, Utah, Mexico, and Alberta, Canada (Muesebeck, et al. 1951). Butler and Werner (1960) have reviewed the pertinent literature regarding parasitism by T. utahensis in eggs of Chlorochroa sayi Stål, Euschistus impictiventris Stål, and Thyanta pallido-virens spinosa Ruckes, all of which commonly appear in Arizona. Other pentatomid hosts are Chlorochroa ligata (Say) and Euschistus servus (Say) (Muesebeck, et al. 1951).

During the middle and late summer of 1966, Chlorochroa uhleri Stål, a pentatomid closely related to C. sayi, was found in large numbers feeding on grain sorghum, alfalfa, and cotton in southern Arizona. It became evident that eggs of this pentatomid also were susceptible to attack by T. utahensis. Since parasitization of C. uhleri by this parasite is not mentioned in the literature, the following research was undertaken

to evaluate this relationship in comparison with that of a second host, C. sayi, and to study further aspects of the biology of the parasite.

The duration of development of T. utahensis in C. uhleri eggs was determined in relation to temperature and compared with the time required for development in C. sayi eggs. Incubation time of C. uhleri eggs in relation to temperature has not been reported and was therefore determined. Comparisons with data on the length of parasite development were then made. Further studies included the calculation of percentage of parasitism obtained in the laboratory and from field-collected eggs, and the ability of T. utahensis to parasitize eggs of C. uhleri and C. sayi of various ages at different temperatures. Data on the total number of eggs that individual females were capable of parasitizing was also obtained. Final considerations included a summary of parasite F_1 sex ratios, and an experiment to determine the effect of feeding on adult male longevity.

MATERIALS AND METHODS

Description of Temperature Cabinets

Six modified 11 ft.^{3} household refrigerators were used as temperature control cabinets and were programmed to operate at 59°, 68°, 77°, 81°, 86°, and 95° F. Two Fenwall thermo-switches adjusted two degrees above and below the programmed temperature controlled the heating and cooling cycles in each cabinet. Heat for each cabinet was supplied by a 75-watt nichrome wire coil (Eagle Cone Glocoil), and the cooling supplied by the intact refrigeration unit. Air was circulated by a Calrad ventilation motor (Model A.C.M.) turning a 2.5 inch fan. A Honeywell humidity control regulated the operation of a small electric fan above a shallow pan of water and maintained the relative humidity between 40 and 60% in each cabinet. Two 15-watt cool-white fluorescent lamps per cabinet provided continuous illumination for 15 hours daily, beginning at 6 A.M.

Cabinet temperature was monitored on a twice-daily basis by the use of a temperature potentiometer (Leeds and Northrup Co., Cat. no. 8692) connected to thermocouples in each cabinet. Several recording

thermometers (Electric Auto-Lite Co., Model 100) also became available from time to time and were used to make continuous 24-hour recordings in the various cabinets. A summary of these temperature data indicates that fluctuations of 0.7 - 1.8°F. above and below the six programmed temperatures existed during the experiment.

Establishment and Maintenance of Host Cultures

Adults of C. uhleri and C. sayi were collected during the early morning and late afternoon hours from July through September in the Tucson, Marana, and Casa Grande agricultural areas. A standard insect sweep net was used for sampling in alfalfa, grain sorghum, cotton, and in the weeds bordering the fields. Chlorochroa uhleri was the predominant species collected in all areas.

Eggs were obtained from C. uhleri laboratory culture units of 25 to 30 females and 10 to 15 males maintained in each of a series of one-gallon glass jars. Each group was supplied with approximately ten green beans for food and two regular-sized paper table napkins crumpled into a loose ball. The napkins provided ample surface area to prevent crowding and were the favored substrate for egg deposition. As the beans began to lose their succulence, they were replaced with a fresh supply.

At the same time any dead C. uhleri were removed to prevent fungus growth. All jars were kept at room temperature.

The same method was used in the maintenance of C. sayi cultures.

Removal and Treatment of Host Eggs

Egg masses were removed daily by cutting out the portion of the napkin to which they were attached. Individual masses were then placed in two-inch plastic petri dishes and the number of eggs counted. Each dish was coded and stored at a particular temperature until the eggs reached the desired age for use in the parasitization study. To determine parasitization and rate of development in host eggs less than one day old, eggs were used immediately; otherwise they were kept in various temperature cabinets until one, two, three, or four days old. Egg masses of C. uhleri not used for the parasitization experiments were retained at the various temperatures and their incubation time recorded. An insufficient egg supply prohibited the determination of C. sayi incubation time under these conditions.

Establishment and Maintenance of T. utahensis Cultures

Adult T. utahensis were collected from areas of high pentatomid populations with a D-Vac vacuum insect net

and stored in the laboratory at the six temperatures in one-ounce plastic cups. Host egg-masses were also collected quite frequently from the hand net sweepings and were held in the cups at 77°F. Emergence of T. utahensis from field-collected eggs was recorded and the parasites distributed among the six cabinets so that cultures of equal size were established at each.

Parasitization of Host Eggs

One female T. utahensis from a culture established at a particular temperature was introduced into a petri dish containing host eggs that had reached the desired age for parasitization at that temperature. A microaspirator (Stoner and Butler 1965) was used for handling the parasites. Each individual was allowed to remain with the egg mass in the temperature cabinet for 24 hours. At the end of this period, the parasite was removed and placed in another petri dish with a second egg mass of the same age and incubated at the same temperature. The time allowed for oviposition was again 24 hours. This procedure was continued until the parasite died.

The parasitized egg masses were checked daily and the sex and number of emerging adults recorded. The time of parasite development was counted from the end of the

24-hour oviposition period to emergence, and recorded in days. When emergence appeared to be complete, the egg mass was removed and normal-appearing eggs examined for unemerged parasites. This was done under a dissecting microscope by removal of egg caps and examination of the egg contents. Pupae and unemerged adults were readily visible. Progeny (F_1) were not removed from the temperature cabinet in which they were reared but were retained to serve as fresh cultures for further parasitization at that temperature.

Statistical Methods

The mean ($\bar{X}$) and standard deviation from the mean (SD) were the statistical tools used for summarizing and comparing data on the number of days required for parasite development, duration of *C. uhleri* egg incubation, and the number of eggs parasitized by individuals. The relationship between the rate of development (reciprocal of days, $\hat{Y}$) and temperature can be expressed as a typical sigmoid curve. Linear regression equations ($\hat{Y} = a + bX$) were calculated for observed data on the straight portions of the sigmoid curves and regression lines plotted from these equations. Coefficients of determination (R^2) gave

an indication of the strength of the relation between the two variables in this range.

RESULTS AND DISCUSSION

Development of T. utahensis in C. uhleri Eggs

The duration of development of T. utahensis in C. uhleri eggs was determined for 4,149 adults that emerged from eggs of various ages parasitized in the laboratory. The results are shown in Table 1.

When the eggs were less than one day old at the time of parasite oviposition, the developmental period ranged from 20.4 (± 2.1) days at 68° to 7.0 (± 0.4) days at 95°F. When the age of the eggs was increased to one and two days, the time required to complete development remained virtually unchanged. Telenomus utahensis could not successfully parasitize host eggs that were three or four days old at 86° and 95°F. Under these conditions, host hatching usually began during the parasite's 24-hour oviposition period. Three- and four-day-old eggs could be parasitized if they had been incubated at temperatures below 86°F. Developmental periods at these lower temperatures were not different from those in the younger host eggs.

Morrill (1907b) states that T. utahensis is capable of parasitizing eggs successfully up to the time

Table 1.--Length of development (in days[1]) of *T. utahensis* in various-aged *C. uhleri* eggs at five constant temperatures.

	Age of Host Eggs									
	<1 day		1 day		2 days		3 days		4 days	
Temp. (°F.)	No.	Mean Days ± SD	No.	Mean Days ± SD	No.	Mean Days ± SD	No.	Mean Days ± SD	No.	Mean Days ± SD
95°	145	7.0±0.4	273	6.9±0.5	11	7.0±0.7	-	-	-	-
86°	400	7.6±0.8	322	7.2±0.5	171	8.0±0.6	-	-	-	-
81°	429	8.8±0.6	263	9.1±0.4	263	9.2±0.8	106	9.4±0.7	24	9.7±0.6
77°	253	10.9±0.6	213	11.1±0.5	396	10.9±0.9	242	11.3±0.7	8	11.8±0.8
68°	270	20.4±2.1	235	21.3±1.1	86	22.4±0.9	39	20.4±1.1	-	-

$\hat{Y} = -0.2673 \pm 0.00466X$[2]

$R^2 = 0.99$[3]

$\hat{Y} = -0.2985 \pm 0.00506X$

$R^2 = 0.99$

$\hat{Y} = 0.2607 \pm 0.00453X$

$R^2 = 0.99$

1/ Days counted from end of 24-hour oviposition period to emergence of F_1 adults.
2/ Regression equation where $\hat{Y}$ equals reciprocal of days and X equals temperature.
3/ Coefficient of determination.

that host embryos have completed one-half of their incubation period and that after this time results are uncertain. Tables 1 and 6 show that C. uhleri eggs that have completed one-half of their incubation period may be parasitized, but that the percentage of parasitism is somewhat reduced. Chlorochroa uhleri eggs require 5.1 (±0.7) days for incubation at 81°F. and 6.3 (±1.1) days at 77°F. Four-day-old eggs were parasitized at the rate of 33.3 and 10.9 per cent, respectively, at these two temperatures. The low percentages indicate the inability of most T. utahensis larvae to stop host embryo development, but they further indicate either that a few larvae have such a capability or that host development had stopped for some other reason.

Although no emergence occurred from C. uhleri eggs incubated at 59°F., parasitization of the various-aged eggs was taking place. Egg masses were kept at this temperature for periods ranging from 28 to 45 days (unparasitized host incubation at this temperature is 12.7 [±1.0] days). Dissections revealed T. utahensis development to the pupal stage in only two of over 700 eggs. However, when parasitized egg masses were moved to the 86°F. temperature cabinet and exposed for periods of 7 to 13 days, dissections revealed that 50 per cent of the parasites had completed development to the pupal stage. Parasite emergence did not occur even though the

parasitized eggs were held beyond the normal period of development.

Development of T. utahensis in C. sayi Eggs

Since C. sayi was not as readily collected as C. uhleri during the test period, T. utahensis development in eggs of this host could not be as extensively studied. Results that were obtained for the 844 emerging adults are presented in Table 2.

Again it was observed that as temperature increased, the time to complete development decreased and that at 59°F. no emergence occurred. In eggs less than one day old, the period of development was 19.1(±1.7) days at 68°F., decreasing to 6.3(±0.4) days at 95°F. In one-day-old eggs, the duration did not change at the temperatures for which data could be obtained. The duration of development in two-day-old C. sayi eggs at 68°F. also appeared to be similar to that for the less-than-one-day-old eggs at this temperature.

Development of T. utahensis took place at 59°F. in several egg masses, but as was the case with C. uhleri eggs, no emergence occurred. However, unlike the situation with C. uhleri, removal of parasitized egg masses to a higher temperature resulted in parasite

Table 2.--Length of development (in days[1/]) of T. utahensis in various-aged C. sayi eggs at five constant temperatures.

	Age of Host Eggs					
	<1 day		1 day		2 days	
Temp. (°F.)	No. Individ.	Mean days ± SD	No. Individ.	Mean days ± SD	No. Individ.	Mean days ± SD
95°	49	6.3±0.4	20	6.6±0.5	-	-
86°	101	6.9±0.7	112	7.0±0.2	-	-
81°	49	8.4±0.5	67	8.8±0.5	-	-
77°	126	10.2±0.8	-	-	-	-
68°	92	19.1±1.7	-	-	228	21.1±0.8

$\hat{Y} = -0.2976 + 0.00514X$[2/]

$R^2 = 0.99$[3/]

1/ Days counted from end of 24-hour oviposition period to emergence of F1 adults.

2/ Regression equation where $\hat{Y}$ equals reciprocal of days and X equals temperature.

3/ Coefficient of determination.

emergence. This occurred in two one-day-old egg masses that had remained at 59°F. for 20 days. After being transferred to the 86°F. temperature cabinet, two parasites emerged from one egg mass and five from the second after a six-day exposure period. Emergence occurred on two other occasions from eggs parasitized at the age of two days. These masses were held at 59°F. for 28 days, with emergence occurring on the fourth day of exposure to 86°F. Because emergence occurred at 86°F. before the normal seven-day developmental period had elapsed, development must have been initiated at 59°F.

The time of development of T. utahensis in C. sayi eggs has been studied previously by Caffrey and Barber (1919) and Clancy (1946). In Caffrey and Barber's work, two experiments were conducted, one commencing on August 13 and the other on August 17. Seventeen days were required for development in the first experiment and 26 days in the second. Clancy found that 12 to 17 days were required during October in Yuma, Arizona and that about two weeks were necessary during the summer months. Because temperatures were not given by these authors, comparisons cannot be made with the results of the present study.

Comparison of *T. utahensis* Development in *C. uhleri* and *C. sayi* Eggs

Data on the rate of development of *T. utahensis* in eggs of the two hosts that ranged in age from less than one to one day at the time of parasitization are compiled in Table 3. It appears that the developmental time is not affected by a change in hosts. Although the mean number of days differs, the addition or subtraction of standard deviations brings the differing means to closely agreeing values.

Tables 1 and 2 include the regression equations and coefficients of determination (R^2) calculated for the rate of development (reciprocal of time) in the various-aged eggs of the two hosts. In each case, the coefficient of determination was sufficiently high to indicate a close correlation between temperature and rate of development, a value of one indicating perfect correlation. The regression lines are plotted in Figure 1. Here it is graphically shown that the rate of development increases with an increase in temperature and that the observed rates conform to a linear relationship. It should be noted that the regression equations do not include rates obtained at 95°F. At this temperature the rate of development begins to decrease to form the upper portion

Table 3.--Comparison of developmental periods[1/] of *T. utahensis* in various-aged eggs of *C. uhleri* and *C. sayi* at five constant temperatures.

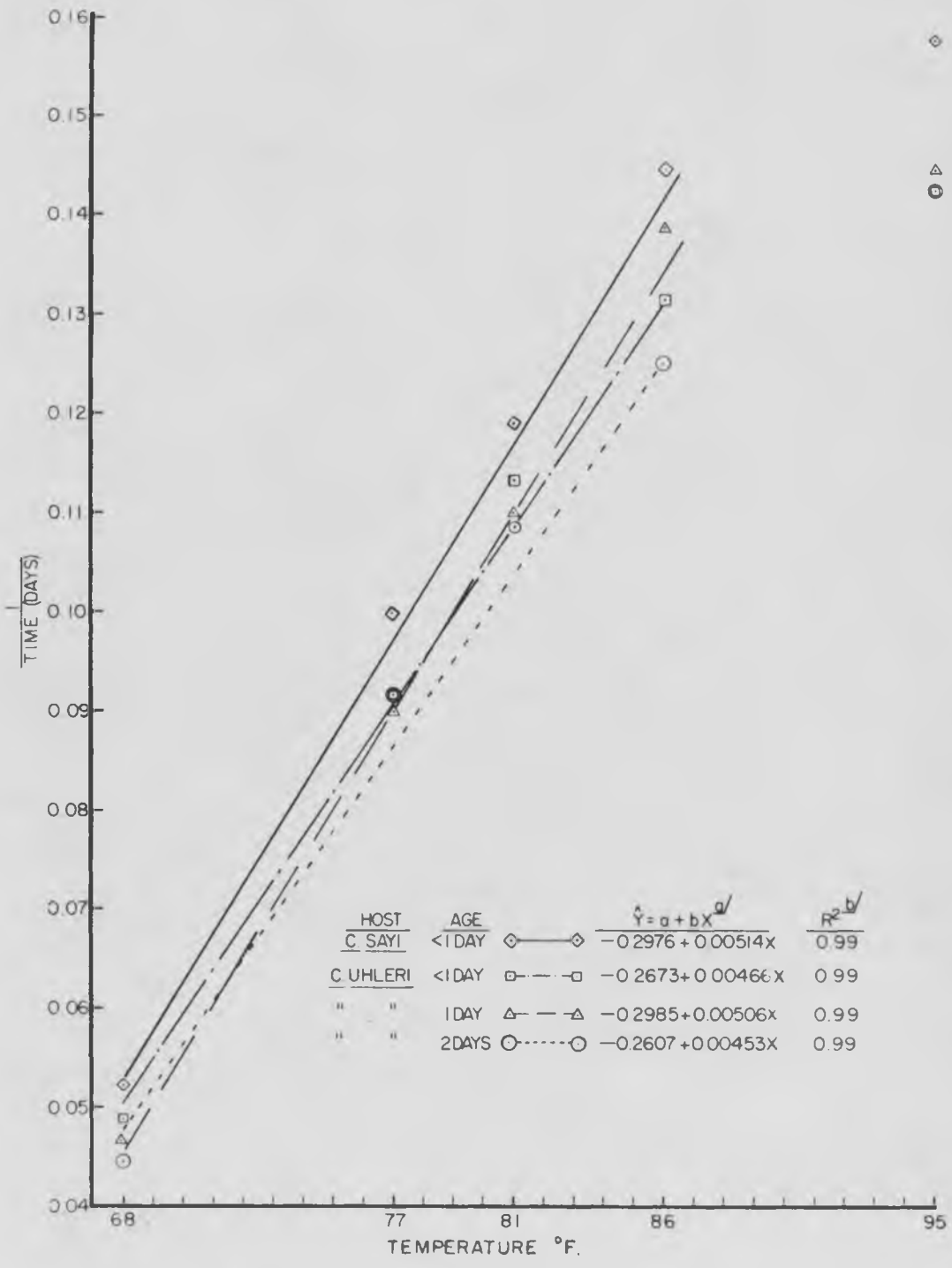
Temp. (°F.)	Age of Host Eggs			
	< 1 day		1 day	
	C. uhleri	*C. sayi*	*C. uhleri*	*C. sayi*
95°	7.0±0.4	6.3±0.4	6.9±0.5	6.6±0.5
86°	7.6±0.8	6.9±0.7	7.2±0.5	7.0±0.2
81°	8.8±0.6	8.4±0.5	9.1±0.4	8.8±0.5
77°	10.9±0.6	10.2±0.8	11.1±0.5	-
68°	20.4±2.1	19.1±1.7	21.3±1.1	-

1/ Mean days ± SD.

Figure 1.--Relation between temperature and rate of development of *T. utahensis* in various-aged *C. uhleri* and *C. sayi* eggs.

a/ Regression equation where $\hat{Y}$ equals reciprocal of days and X equals temperature.

b/ Coefficient of determination.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TEMPERATURE °F.
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AGE
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R² b/
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−0.2976 + 0.00514X
0.99
C. UHLERI
<1 DAY
−0.2673 + 0.00466X
0.99
" "
1 DAY
−0.2985 + 0.00506X
0.99
" "
2 DAYS
−0.2607 + 0.00453X
0.99

Figure 1.

of the sigmoid curve. Rates of development at temperatures ranging from 68° to 86°F. may be interpolated on the plotted straight portions of these sigmoid curves. The closeness of the lines indicates the similarity in the rates of development of T. utahensis in the two hosts regardless of age.

Incubation Time for C. uhleri and C. sayi Eggs

The duration of C. uhleri egg incubation periods at six temperatures are presented in Table 4. Hatching occurred in 4.0 (±0.3) days when the eggs were incubated at 95°F. and in 4.2 (±0.7) days at 86°F. An additional day was required at 81°F. and approximately two more at 77°F. At 68° and 59°F., the number of days increased to 10.0 (±1.8) and 12.7 (±1.0), respectively.

Although C. sayi incubation periods were not determined in this experiment, data have been recorded by Russell (1952), Patton and Mail (1935) and Caffrey and Barber (1919). Studies by Patton and Mail at 60°, 71°, 82°, and 89°F. showed that C. sayi incubation required 14, 8, 6, and 4 days, respectively, as compared to Russell's findings of 10, 6.2, and 5 days at temperature ranges of 60-70°, 70-80°, and 80-90°F., respectively. Caffrey and

Table 4.--Duration of incubation period (in days[1/]) and per cent hatch of *C. uhleri* eggs at six constant temperatures.

Temp. (°F.)	No. eggs incubated	No. eggs hatched	Mean days ± SD	Per cent hatch
95°	439	289	4.0±0.3	65.8
86°	345	171	4.2±0.7	46.7
81°	357	209	5.1±0.7	58.5
77°	450	243	6.3±1.1	54.0
68°	164	74	10.0±1.8	45.1
59°	1633	1062	12.7±1.0	65.0

$$\hat{Y} = -0.4281+0.00771X$$ [2/]

$$R^2 = 0.99$$ [3/]

1/ From time of deposition to hatch.

2/ Regression equation where $\hat{Y}$ equals reciprocal of days and X equals temperature.

3/ Coefficient of determination.

Barber had found the incubation time to be 7 and 4 days at 70° and 90°F., respectively.

Incubation periods of C. uhleri at 68°, 77°, and 86°F. agree to within less than one-half day with those recorded by Russell for C. sayi. Differences of one to four days exist between the data obtained for C. uhleri and those obtained by Patton and Mail, and by Caffrey and Barber for C. sayi at the various temperatures.

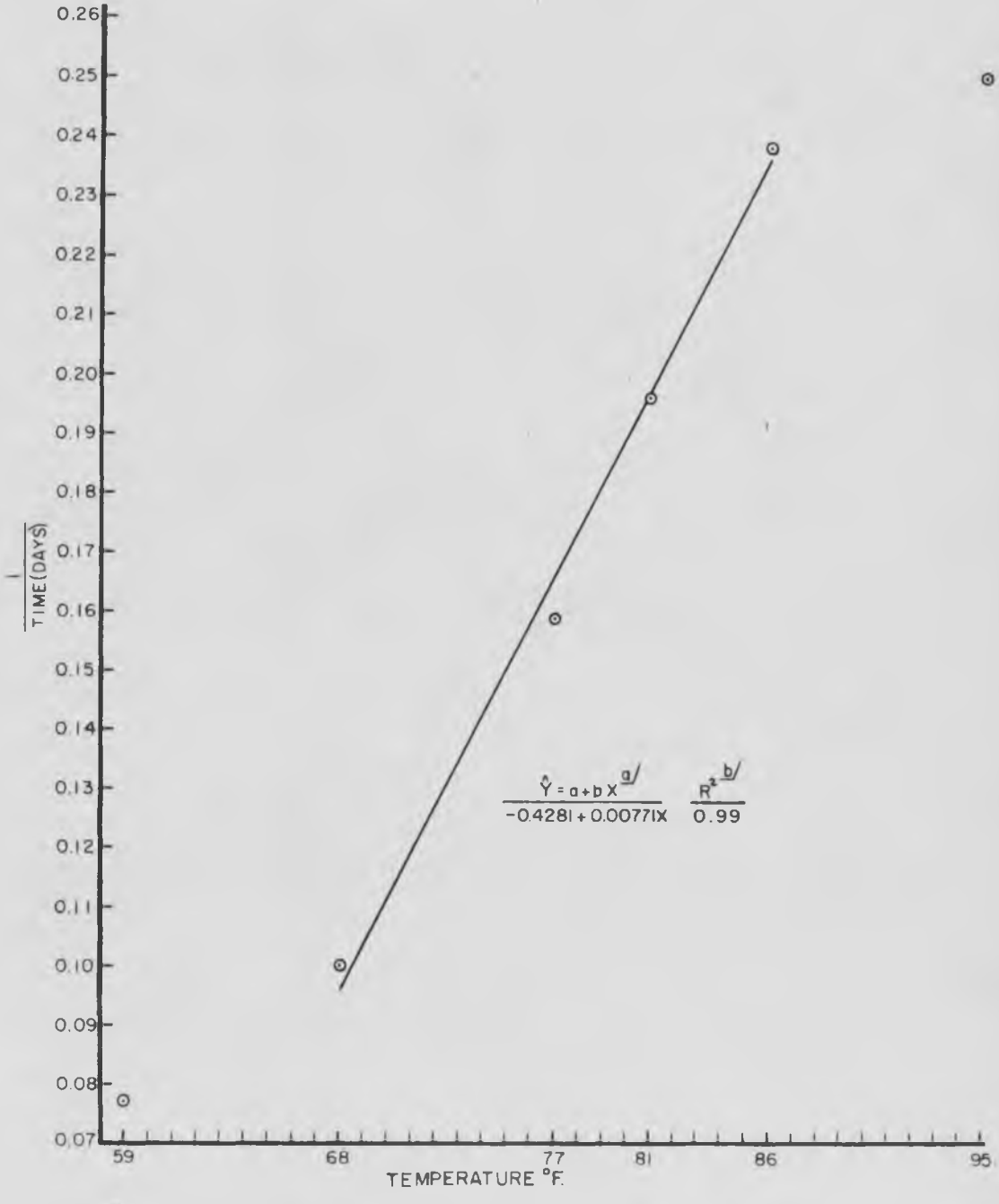
The per cent of C. uhleri eggs that hatched at each of the six temperatures is recorded in Table 4. Per cent hatch was highest at 59° and 95°F. and lowest at 68° and 86°F. Of the 3,388 C. uhleri eggs incubated in this study, 2,038 hatched, 60.2% of the total. Russell (1952) recorded a hatch of 62% from 65,551 C. sayi eggs field-collected in Arizona between 1936 and 1942. A higher percentage of hatching was found by Caffrey and Barber (1919) in C. sayi eggs collected in New Mexico; of the 1,068 eggs collected, 981 eggs or 91.9% of the total hatched.

A linear regression equation was calculated for the C. uhleri egg incubation rates that make up the straight portion of the rate-temperature curve. The equation is given in Table 4 and the line plotted in Figure 2. Developmental rates at 59° and 95°F. are not included since they represent areas of decreasing rates on

Figure 2.--Relation between temperature and *C. uhleri* egg incubation rate.

a/ Regression equation where $\hat{Y}$ equals reciprocal of days and X equals temperature.

b/ Coefficient of determination.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1/TIME(DAYS)
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68
77
81
86
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TEMPERATURE °F.
Ŷ = a+bX a/ -0.4281 + 0.00771X
R² b/ 0.99

Figure 2.

the sigmoid curve. A coefficient of determination of 0.99 indicates a close relationship between the data and the calculated regression line.

Comparison of C. uhleri Incubation and T. utahensis Developmental Times

The number of days for C. uhleri egg incubation and the time required for T. utahensis to complete development are compared in Table 5. At the five temperatures at which T. utahensis emerged, the parasite required approximately 1.8 times longer to develop than the host when the eggs were parasitized at an age of less than one day. Although excluded from the Table, parasite development in eggs parasitized at the ages of one and two days required approximately 2.2 times longer than that of the unparasitized host egg.

Morrill (1907b) made a similar comparison with T. utahensis (reported as T. ashmeadi) developing in eggs of C. ligata at 80.2°, 76°, 74°, and 69.8°F., but did not give data on the age of the host eggs at the time of parasitization. His data show that the parasite required "about twice the normal incubation period of the host egg."

Table 5.--Comparison of C. uhleri egg incubation and T. utahensis developmental periods (in days) at six constant temperatures.

Temp. (°F.)	C. uhleri eggs mean days ± SD	T. utahensis[1/] mean days ± SD
95°	4.0±0.3	7.0±0.4
86°	4.2±0.7	7.6±0.8
81°	5.1±0.7	8.8±0.6
77°	6.3±1.1	10.9±0.6
68°	10.0±1.8	20.4±2.1
59°	12.7±1.0	No emergence

1/ Development in C. uhleri eggs parasitized when less than one day old.

Parasitization Capabilities

Difficulty in determining per cent parasitism

The difficulty in determining the number of eggs actually parasitized by T. utahensis has been discussed by Morrill (1907a, b, 1910). Obviously, the number of emerged adults gives only a partial indication of the total number of parasitized eggs since unemerged parasites in the form of immature stages and fully-developed adults are usually present. It becomes necessary to count these stages in order to ascertain true parasitization capabilities. Removal of egg caps reveals adults and various-aged pupae, but parasite larvae are difficult to find. Nevertheless, a pentatomid egg failing to hatch could have been destroyed by a feeding larva that had ceased development in the early stages. Morrill (1910) states that eggs failing to hatch are usually destroyed by parasites and that "these eggs contain nothing but a shriveled, brownish, and structureless mass." It was noted in the present study, however, that unparasitized eggs have a similar internal appearance if development had ceased in the early embryonic stages. Therefore, it cannot be assumed that an egg has been parasitized if its internal appearance resembles Morrill's description.

In the following discussion of T. utahensis parasitization, data on the per cent of available eggs parasitized or the number of eggs parasitized by individuals are calculated from the number of emerged adults plus observable unemerged stages. It can be assumed that eggs that had neither hatched nor been parasitized had either been destroyed by parasite larvae that had ceased development, or were not viable for other reasons.

Per cent parasitism in the laboratory

In order to evaluate the ability of T. utahensis to parasitize various-aged C. uhleri and C. sayi eggs at the five temperatures, percentages of parasitism were calculated. Results obtained from C. uhleri eggs are presented in Table 6. Per cent parasitism was highest in less-than-one-day- and one-day-old eggs and generally decreased as the age of the egg increased. Percentages were highest at 81° and 86°F. in less-than-one-day-old eggs; 77.1 and 79.8%, respectively, were recorded. The percentages of hatch of C. uhleri nymphs from the partially parasitized egg masses are also given in Table 6. By adding these figures to the per cent parasitism, it is found that 78.8% of all eggs either hatched

Table 6.--Per cent parasitization of various-aged *C. uhleri* eggs by *T. utahensis* at five constant temperatures.

Temp. (°F.)	Age of host eggs	No. female parasites used	No. host eggs	No. emerged F_1 adults	No. parasites not emerged[1/]	% parasitism %emerged	% parasitism %total	% host hatch
95°	< 1 day	6	219	145	2	66.2	67.1	12.3
	1 day	15	536	273	10	50.9	52.8	31.5
	2 days	10	542	11	6	2.0	3.1	71.5
86°	< 1 day	10	524	400	18	76.3	79.8	7.1
	1 day	13	589	322	7	54.7	55.8	18.3
	2 days	10	358	171	5	47.8	49.2	31.0
81°	< 1 day	10	559	429	2	76.7	77.1	8.6
	1 day	15	543	263	6	48.0	49.5	35.0
	2 days	10	536	263	1	49.1	49.2	13.5
	3 days	9	358	106	4	29.6	30.7	40.3
	4 days	2	72	24	0	33.3	33.3	26.4
77°	< 1 day	10	539	253	2	46.9	47.3	35.1
	1 day	9	386	213	9	55.2	57.5	29.2
	2 days	13	682	396	2	58.1	58.4	30.1
	3 days	12	624	242	4	38.8	39.4	38.8
	4 days	2	92	8	2	8.7	10.9	64.2
68°	< 1 day	10	473	270	4	57.1	57.9	24.5
	1 day	13	868	235	2	27.1	27.3	52.3
	2 days	4	177	86	1	48.6	49.2	28.8
	3 days	5	404	39	3	9.6	10.4	55.5

1/ Includes adults and pupae.

normally or were visually determined to be parasitized. The remaining 21.2% could have been infertile or successfully parasitized by larvae that did not mature.

The results of a similar study of per cent parasitization of C. sayi are shown in Table 7. Maximum per cent parasitism was similar to the maximum that occurred in less-than-one-day- and one-day-old C. uhleri eggs; however, decreasing percentages due to increases in host age are not obvious. The maximum percentage of C. sayi eggs parasitized was 79.7%, in less-than-one-day-old eggs at 77°F. A combination of data on per cent parasitism and hatch of C. sayi eggs again showed that approximately 21% were either infertile or destroyed by parasites that did not reach an age where they could be observed.

Caffrey and Barber (1919) and Morrill (1907b) observed that nymphs rarely hatched from egg masses that produced parasites. As mentioned previously, nymphs frequently hatched from partially parasitized egg masses in this study. It seems quite obvious that a fertile egg not attacked by a parasite will develop, regardless of the condition of adjacent eggs.

Per cent parasitism in the field

Morrill (1907a) collected 427 C. ligata and C. sayi eggs from the field at Barstow, Texas and observed

Table 7.--Per cent parasitization of various-aged C. sayi eggs by T. utahensis at five constant temperatures.

Temp. (°F.)	Age of host eggs	No. female parasites used	No. host eggs	No. emerged F_1 adults	No. parasites not emerged 1/	% parasitism %emerged	% parasitism %total	% host hatch
95°	< 1 day	5	106	49	0	46.2	46.2	20.7
	1 day	3	36	20	0	55.6	55.6	36.1
86°	< 1 day	5	152	102	5	67.1	70.4	14.5
	1 day	10	219	112	3	51.1	52.5	26.0
81°	1 day	5	140	49	0	35.0	35.0	40.0
	1 day	6	145	67	0	46.2	46.2	24.1
77°	< 1 day	6	158	126	0	79.7	79.7	17.7
68°	< 1 day	5	203	92	3	45.3	46.8	37.4
	1 day	3	63	2	1	3.2	4.8	47.6
	2 days	8	313	227	4	72.5	73.8	12.8

1/ Includes adults and pupae.

that 13% hatched and 14% produced adult T. utahensis. Dissection of ten eggs from the remaining 43% revealed that a dead adult parasite was present in each. In a later publication (Morrill 1910), he summarized parasitism data for 1,221 C. ligata eggs that were field-collected in western Texas during 1905. Telenomus utahensis emerged from 55.5% of this number and 14% hatched. He then concluded that "the total percentage of conchuela [C. ligata] eggs destroyed by Proctotrypid parasites is from 15 to 25% above the percentage . . . from which parasites actually matured and emerged."

Per cent parasitism by T. utahensis in the field has been recorded by other authors, but detailed host-hatching data do not accompany their percentages. Caffrey and Barber (1919) recorded a 60% parasite emergence from C. sayi eggs collected in Arizona during the latter part of July and early August. A 66% emergence was recorded by Russell (1952) from late summer collections of C. sayi eggs. Clancy (1946) collected 1,399 Euschistus impictiventris eggs in Arizona during 1937 and found that approximately 23% were parasitized. Early-season (July 20) collections of C. sayi eggs near Yuma showed that only 6.9% of 1,704 produced parasites, six of which were Ooencyrtus johnsonii (Hymenoptera: Encyrtidae). Later in the season (Oct. 4), 664 field-collected eggs were

determined to be parasitized by Telenomus podisi Ashmead and T. utahensis at the rate of 95.9%.

In the present study, 2,039 C. sayi and C. uhleri eggs were collected between August 9 and September 8 in the vicinity of Casa Grande and Tucson. From these, 1,040 T. utahensis emerged. This is a 51% emergence, lower than the 60% recorded by Caffrey and Barber but similar to 55.5% recorded by Morrill in C. ligata eggs from western Texas.

Individual parasitization capacity

Telenomus utahensis egg-laying capacity was considered in this study. However, due to the difficulties in determining total egg production or the total number of eggs parasitized, it was not possible by the methods used to obtain the most accurate data. Therefore, Table 8 shows the mean number of eggs parasitized as based on the number of emerged adults plus observable unemerged stages. Generally, individual wasps parasitized a greater number of C. uhleri eggs. The highest numbers parasitized were 66, 65, and 60 in less-than-one-day-old eggs held at 86°, 81°, and 77°F., respectively. In C. sayi eggs, the greatest number parasitized was only 51 (less-than-one-day-old eggs held at 68°F.). The mean number of C. uhleri eggs parasitized was higher than the number of

Table 8.--Number of various-aged C. uhleri and C. sayi eggs parasitized by individual T. utahensis at five constant temperatures.1/

Temp. (°F.)	Age of host	C. uhleri No. Individ.	C. uhleri No. Parasitized Range	C. uhleri No. Parasitized Mean	C. sayi No. Individ.	C. sayi No. Parasitized Range	C. sayi No. Parasitized Mean
95°	< 1 day	6	14-37	24.3	5	12-25	16.3
	1 day	15	8-46	23.5	3	8-12	10.0
	2 days	10	2-7	3.4	-	-	-
86°	< 1 day	10	12-66	42.1	5	8-46	26.5
	1 day	13	12-53	27.5	10	7-36	14.4
	2 days	10	14-35	22.0	-	-	-
81°	< 1 day	10	18-65	43.7	5	8-29	16.3
	1 day	15	11-39	20.6	6	13-30	16.7
	2 days	10	2-53	33.1	-	-	-
	3 days	9	3-35	13.3	-	-	-
77°	< 1 day	10	3-60	31.0	6	9-30	21.0
	1 day	9	4-51	31.5	-	-	-
	2 days	13	13-54	36.9	-	-	-
	3 days	12	1-51	22.7	-	-	-
68°	< 1 day	10	7-57	28.2	5	21-51	31.6
	1 day	13	3-55	26.4	-	-	-
	2 days	4	16-34	21.7	8	6-32	28.8
	3 days	5	1-20	10.5	-	-	-

1/ Data based on the number of emerged and unemerged adults and visible unemerged stages.

C. sayi eggs at 77°, 81°, 86°, and 95°F. but was slightly lower at 68°F. The maximum mean number of C. uhleri and C. sayi eggs parasitized was 43.7 at 81° and 31.6 at 68°F., respectively.

Morrill (1907b) also made a study of the maximum number of eggs that could be successfully parasitized by one female T. utahensis. The highest number he observed was 27, but he was careful to point out that "this number could be greatly exceeded."

Tables 10 through 14 in the appendix are included so that further study of individual female performance may be pursued. These tables record the number of various-aged C. uhleri or C. sayi eggs made available to each female, the number observed to be parasitized, and the number that hatched (at the five temperatures). Sex ratios of the F_1 progeny are discussed elsewhere. The variation in the number of eggs parasitized is evident, as is the potential of many individuals.

In Table 10, for instance, Female U218 (86°F.) appeared to have successfully parasitized 66 of 81 eggs. Since 13 C. uhleri hatched from these 81 eggs, only two are left unaccounted for. They could have been parasitized, and if so, U218's best possible performance in the test would have been 68 eggs parasitized. Likewise, Female U191 (81°F.) parasitized 65 of 95 eggs.

Only three C. uhleri eggs hatched, indicating that the remaining 27 might have been parasitized. If this were the case, U191 successfully parasitized 92 eggs. Similar examples can be drawn from the other tables, and it becomes obvious that before any exact egg-laying data can be obtained, rigorous observation techniques will have to be employed and the parasite given the optimum conditions for parasitization.

Adult Longevity

An attempt was not made in this study to consider what factors other than temperature and host age contribute to an ideal situation for parasitization. It became evident, however, that the availability of food would be an important factor. Throughout this study females confined in petri dishes had no available food or moisture source other than the host egg mass. Approximate adult female longevity under these conditions was from one to eight days. Female U219 (Table 10, 86°F.) died exactly three days after emergence. During this period, she parasitized 65 eggs available to her. It is possible that she could have parasitized an additional number of eggs if she had lived longer.

In a separate experiment, it was indicated that the availability of food increases longevity. Since the females were being utilized in the parasitization experiments, only males were tested. These were placed in individual two-inch plastic petri dishes as soon as they emerged from eggs that had been parasitized at the various temperatures. The data from this experiment are shown in Table 9. If no food or moisture source was provided, mean longevity ranged from 2.1 days at 95° to 11.2 days at 59°F. At the mid-range temperatures of 77° and 81°F., the longevity was 4.3 and 4.8 days, respectively. When small strips of filter paper soaked in honey-water were made available, longevity was increased considerably. At 95°F., the greatest longevity was 15 days and the mean for the test group was five. Longevity was increased to a mean of 13.9 days, with a peak of 35, when food was supplied at 81°F. An even greater increase in longevity was obtained under these conditions at 77°F.; at this temperature the two males tested lived for 46 and 58 days, respectively.

It has been demonstrated (Hodson, 1939) that the longevity of another Telenomus species, T. clisiocampae Riley, a parasite of the forest tent caterpillar, can be increased in the laboratory when food is

Table 9.--Longevity of virgin T. utahensis males with and without honey-water at six constant temperatures.

Temp. (°F.)	Honey-water absent			Honey-water present		
	No. Individ.	Days		No. Individ.	Days	
		Range	Mean		Range	Mean
95°	10	2-3	2.1	10	3-15	5.0
86°	10	3-4	3.3	-	-	-
81°	6	4-5	4.3	10	3-35	13.9
77°	9	4-5	4.8	2	46-58	47.0
68°	10	5-9	7.2	-	-	-
59°	10	10-13	11.2	-	-	-

made available. Hodson found that when moistened raisins were provided, longevity increased from 4.0 to 15.5 days at 68°F. and from 4.5 to 14.6 days at 59°F. There was a half-day decrease at 50°F. from 6.0 to 5.5 days.

Morrill (1907b) stored T. utahensis adults in glass tubes, pill boxes, and insect cages. No food was made available other than the egg mass and the dried cotton leaf to which the mass was attached. Under these conditions, average longevity was 3.8 days, with a maximum of eight. He concluded that

> parasites are sufficiently nourished during their larval existence to require no food for carrying on, at least to a certain extent, their reproductive functions. It is not unlikely, however, that their longevity and reproductive capacity is increased by such food as they might obtain under natural conditions.

In laboratory work with another scelionid parasite, Ascolus basalis (Wollaston), Cumber (1964) found that adults lived and bred readily in the absence of food.

Sex Ratios of F_1 Progeny

As previously mentioned, Tables 10 through 14 present the sex ratios of emerged F_1 progeny. A summary of all sex ratio data from parasitized C. uhleri eggs (in all various-aged eggs at all temperatures) revealed

that of the 4,117 emerged parasites, 25.2% were males and 74.8% were females. Of the 417 T. utahensis adults that emerged from C. sayi eggs (all less than one day old), 44.6% were males and 55.4% females.

Morrill (1907b) found that from field-collected pentatomid eggs, 15% of the emerged parasites were males and 85% females. On the other hand, in laboratory experiments 89% of F_1 progeny were males and only 11% females. His breeding experiments indicated that parthenogenic development probably occurs in T. utahensis, and resulted in the high percentage of males. Presumably, the females had had a lesser chance of becoming fertilized than in the field. It does seem likely that opportunities for fertilization in the laboratory cultures were unusually high during the present studies. Several males normally emerged from every parasitized egg mass before female emergence and remained close to or on the egg mass. Wilson (1961) observed a similar behavior in Ascolus basalis (Hymenoptera: Scelionidae) emerging from pentatomid eggs. He states that this allows for immediate mating with each female on emergence.

Certain data from the present experiments tend to strengthen Morrill's contention that parthenogenic reproduction occurs in T. utahensis. Many females, e.g.

U83, U84, U85, U86, and U87 (Table 11, 86°F.), produced male progeny only. Although it would appear that offspring of these females had developed parthenogenetically, I wish to stress that throughout this study no attempt was made to observe whether these or other females had mated.

In most Hymenoptera, females develop from fertilized eggs while males develop from unfertilized eggs. A few species of Scelionidae have been tested for parthenogenic reproduction; according to Clausen (1962) and Sweetman (1963) only male progeny result. Based on the present data, however, it cannot be concluded without qualification that parthenogenic development occurs in T. utahensis. Only after deliberate attempts are made to ascertain this reproductive characteristic will it be possible to accept or reject such a hypothesis.

SUMMARY

Telenomus utahensis Ashmead is an important egg parasite of Pentatomidae that attack various Arizona crops. Two hosts, *Chlorochroa uhleri* and *C. sayi*, were commonly found feeding on grain sorghum, alfalfa and cotton in southern Arizona during the summer of 1966. Their eggs were subject to attack by this parasite. A study was undertaken to determine rates of development of *T. utahensis* in relation to temperature in various-aged eggs of these two hosts and to consider further aspects of its biology.

The rates of development were studied at 59°, 68°, 77°, 81°, 86°, and 95°F. in host eggs that varied in age from less than one to four days old. The length of development in both hosts and in all eggs varied inversely with temperature. Parasite development usually did not take place, nor did emergence occur, in any of the various-aged eggs of the two hosts at 59°F. However, when eggs parasitized at 59°F. were moved to the 86° or 95°F. temperature cabinets, development proceeded and emergence oftentimes occurred. The time required to complete development in less-than-one-day-old *C. uhleri* eggs varied from 20.4 (±2.1) days at 68° to 7.0 (±0.4)

days at 95°F. These periods were not changed as the host age was increased to four days; determinations were not made beyond this point. In C. sayi eggs less than one day old, the time required was 19.0 (±1.7) days at 68°F. and ranged to 6.3 (±0.4) days at 95°F. The developmental period did not change as host age increased. Standard deviations were generally higher for development in the two hosts at the lower temperatures, indicating that development varied to a greater extent among individuals. Linear regression equations were calculated for the rates of development, and the lines plotted.

Chlorochroa uhleri egg incubation times have not been reported and were therefore determined at the six temperatures. At 59°F. 12.7 (±1.0) days were required, and at 95°F. the length was reduced to 4.0 (±0.3) days. A linear regression equation was calculated, and the line plotted.

A comparison of C. uhleri egg incubation, and T. utahensis developmental times in this host was made at the various temperatures. The parasite required approximately twice as long to complete its development.

The percentages of various-aged host eggs parasitized at the different temperatures were also calculated. Parasitism was highest (70-80%) in less-than-

one-day- and one-day-old eggs and generally decreased as the age of the eggs increased. The highest percentages were recorded in the 77°-86°F. range. Average over-all per cent parasitism in C. uhleri eggs was approximately 8% higher than in C. sayi eggs. After accounting for all parasitized eggs as well as those from which pentatomids hatched, a segment of the host population--amounting to 21%--remained from which no pentatomids or parasites emerged. It is speculated that these eggs were either parasitized successfully by T. utahensis larvae that ceased development or that the eggs were inviable for other reasons. Parasitism of field-collected eggs of C. uhleri and C. sayi amounted to 51%. However, these eggs were not examined for unemerged parasites; the percentage therefore may have been higher.

The maximum number of eggs individual females were capable of parasitizing under the conditions of this study was 66 C. uhleri and 51 C. sayi. The highest mean number of eggs parasitized by T. utahensis was 43.7 C. uhleri and 31.6 C. sayi. Maximum parasitism always occurred in less-than-one-day-old eggs.

The sex ratio of T. utahensis adults reared from all C. uhleri eggs in the laboratory was 25.2% males and 74.8% females. From all C. sayi eggs, the ratio was 44.6% males and 55.4% females.

Further studies on T. utahensis parasitization capabilities should include a study of female longevity. It is suggested that females in this study may not have exhibited their full potential since food was not made available. An experiment with adult male T. utahensis indicated that longevity in the laboratory could be greatly increased if honey-water is provided.

APPENDIX

Table 10.--Number of available C. uhleri eggs (less than one day old) parasitized, and sex ratios of emerged F_1 progeny produced by T. utahensis at five constant temperatures.

Temp. (°F.)	Individ. female code no.	Host Eggs			Sex ratios emerged F_1 progeny male:female
		No. available	No. parasitized	No. hatched	
95°	U7	68	26	15	2:24
	U8	43	34	0	2:31
	U13	53	37	8	3:34
	U19	14	14	0	2:11
	U20	27	21	5	2:19
	U225	14	14	0	2:12
86°	U1	60	46	10	2:41
	U18	41	37	0	1:36
	U22	18	12	0	0:12
	U23	24	24	0	1:22
	U218	81	66	13	5:58
	U219	65	65	0	7:51
	U221	34	34	0	2:32
	U222	63	47	7	3:41
	U223	52	48	0	3:43
81°	U3	64	44	0	4:40
	U4	114	44	40	2:42
	U17	18	18	0	2:16
	U191	95	65	3	6:59
	U192	58	54	1	4:48
	U193	53	52	0	4:48
	U215	17	16	0	16:0
	U216	60	49	4	49:0
	U217	30	29	0	2:27
77°	U5	81	60	15	3:57
	U6	74	41	33	3:38
	U25	86	52	3	52:0
	U205	34	3	19	3:0
	U206	53	4	21	3:1
	U207	26	26	0	2:24
68°	U9	67	57	6	56:0
	U10	29	7	18	7:0
	U27	90	34	31	4:30
	U28	45	24	18	24:0
	U186	62	38	5	5:33
	U187	16	12	0	11:1
	U188	17	16	0	2:14
	U189	79	42	13	4:38
	U190	25	24	0	2:22

Table 11.--Number of available C. uhleri eggs (one day old) parasitized, and sex ratios of emerged F_1 progeny produced by T. utahensis at five constant temperatures.

Temp. (°F.)	Individ. female code no.	Host Eggs			Sex ratios emerged F_1 progeny male:female
		No. available	No. parasitized	No. hatched	
95°	U90	41	25	2	24:1
	U91	62	8	41	8:0
	U92	53	14	9	12:0
	U120	43	30	9	2:27
	U121	49	46	2	4:39
	U122	29	29	0	2:26
	U127	27	27	0	1:23
	U136	21	20	0	20:0
	U137	17	16	0	15:0
	U139	20	20	0	1:19
	U140	27	16	10	2:13
	U141	40	32	5	4:27
86°	U83	70	18	15	18:0
	U84	24	14	0	14:0
	U85	75	42	12	39:0
	U86	72	33	12	31:0
	U87	64	12	18	11:0
	U124	15	14	0	1:3
	U125	30	14	8	1:12
	U127	24	24	0	1:23
	U130	63	53	5	3:50
	U131	72	51	17	6:45
	U132	48	42	1	5:37
	U133	12	12	0	2:10
81°	U31	68	21	27	4:16
	U33	12	12	0	1:10
	U34	24	24	0	1:23
	U35	54	26	13	1:24
	U55	20	19	0	1:18
	U57	20	16	0	2:14
	U58	11	11	0	1:10
	U59	27	27	0	2:25
	U60	39	39	0	2:36
	U61	53	8	42	0:8
	U62	20	20	0	0:20
	U63	39	29	1	1:28
	U64	44	17	21	0:15
77°	U41	44	41	3	7:34
	U42	71	42	27	4:32
	U65	28	4	18	1:3
	U67	28	21	3	2:19
	U69	28	20	4	2:18
	U134	54	42	5	3:36
	U135	85	51	16	6:45
68°	U43	69	23	35	0:23
	U44	44	30	10	2:27
	U46	20	15	0	2:13
	U108	111	34	45	3:31
	U145	120	55	54	5:50
	U146	96	3	56	0:3
	U168	97	16	43	5:11
	U169	77	23	42	4:19
	U194	58	39	16	4:35

Table 12.--Number of available C. uhleri eggs (two days old) parasitized, and sex ratios of emerged F_1 progeny produced by T. utahensis at five constant temperatures.

Temp. (°F.)	Individ. female code no.	Host Eggs			Sex ratios emerged F_1 progeny male:female
		No. available	No. parasitized	No. hatched	
95°	U48	82	3	46	1:0
	U80	53	2	24	1:0
	U81	29	7	9	1:5
	U88	55	5	45	3:0
86°	U72	36	28	3	2:26
	U77	31	22	5	1:22
	U77a	42	14	13	1:13
	U93	40	35	0	4:31
	U162	27	25	0	1:23
	U163	39	15	7	1:11
	U164	22	22	0	1:21
	U165	38	15	11	-
81°	U149	34	2	21	1:1
	U154	49	25	11	2:23
	U155	67	42	14	4:38
	U156	99	50	39	2:48
	U157	88	53	19	5:47
	U158	57	33	7	4:29
	U159	27	26	0	3:23
	U224	56	34	0	2:31
77°	U70	42	13	11	2:10
	U78	14	14	0	1:13
	U95	42	28	9	3:24
	U96	78	37	29	2:35
	U97	38	35	1	4:31
	U98	48	48	0	4:44
	U99	79	51	19	5:46
	U100	78	54	14	5:49
	U101	47	46	0	4:42
	U102	78	46	26	3:43
	U103	85	34	43	0:34
68°	U161	72	34	33	5:29
	U197	25	17	6	2:15
	U198	18	16	0	3:13
	U199	62	20	12	2:18

Table 13.--Number of available C. uhleri eggs (three days old) parasitized, and sex ratios of emerged F_1 progeny produced by T. utahensis at three constant temperatures.

Temp. (°F.)	Individ. female code no.	Host Eggs: No. available	Host Eggs: No. parasitized	Host Eggs: No. hatched	Sex ratio emerged F_1 progeny male:female
81°	U112	47	35	26	4:30
	U113	46	3	33	1:22
	U114	72	17	23	3:12
	U115	31	4	17	1:3
	U116	10	8	0	2:6
	U117	40	24	9	3:21
	U118	13	5	3	1:3
	U119	73	14	40	1:13
77°	U109	41	23	18	2:21
	U110	14	14	0	1:13
	U147	40	7	19	1:5
	U153	22	1	9	1:0
	U166	87	9	72	1:7
	U174	65	6	28	0:6
	U176	86	51	15	6:45
	U177	35	28	1	2:26
	U178	66	36	16	1:35
	U180	78	43	29	3:40
68°	U210	43	13	2	13:0
	U211	40	8	18	8:0
	U212	78	20	33	20:0
	U213	110	1	59	1:0

Table 14.--Number of available C. sayi eggs (less than one day old) parasitized, and sex ratios of emerged F_1 progeny produced by T. utahensis at five constant temperatures.

Temp. (°F.)	Individ. female code no.	Host Eggs: No. available	Host Eggs: No. parasitized	Host Eggs: No. hatched	Sex ratio emerged F_1 progeny male:female
95°	S10	12	12	0	2:10
	S28	12	12	0	3:9
	S27	25	25	0	2:23
86°	S3	36	8	22	1:7
	S4	41	32	0	4:27
	S18	20	20	0	19:0
	S29	46	46	0	13:30
81°	S2	38	29	6	3:26
	S17	8	8	0	8:0
	S33	14	12	0	12:0
77°	S11	28	15	13	2:13
	S12	29	13	15	3:10
	S13	42	41	0	3:38
	S16	31	30	0	30:0
	S31	10	9	0	9:0
	S32	18	18	0	18:0
68°	S6	44	21	23	4:15
	S15	56	51	3	50:0
	S30	40	23	14	1:22

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