Effects of Temperature on Development and Reproduction in *Euschistus tristigmus tristigmus* (Hemiptera: Pentatomidae) with Notes on Reproductive Behavior[1]

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ABSTRACT

E. t. tristigmus adults were collected in Jackson Co., Illinois, and their offspring reared in the laboratory at 22, 27, or 32°C. The optimal temperature for development appears to be between 27 and 32°C.

The effects of the 3 temperatures on reproduction were also studied. Total and rate of fecundity were highest at 22 and lowest at 32°C; rate decreased over time at the 3 temperatures. Total percent fertility at 22°C was equal to that at 27°C, and higher than at 32°C. Total percent hatch of all eggs was highest at 22 and lowest at 32°C, and of fertile eggs highest at 22 and equal at 27 and 32°C. Oviposition periods were longest at 22 and shortest at 32°C, while preoviposition and postoviposition periods were not affected differently by the 3 temperatures.

Precopulatory and copulatory behaviors were observed between 6 pairs of animals.

INTRODUCTION

The phytophagous pentatomid *Euschistus tristigmus* occurs from northern Canada to southern Mexico (Van Duzee 1904) and includes 2 subspecies: *luridus* Dallas is found north, and *tristigmus* (Say) south, of the 41st parallel (McPherson 1976). Thus *E. t. tristigus* occurs in southern Illinois.

Various aspects of the biology of *E. t. tristigmus* have been studied including life cycle and/or rearing under controlled conditions (Esselbaugh 1948; McPherson 1971, 1975a; Woodside 1946), and role of photoperiod in producing adult dimorphism (McPherson 1974, 1975b, 1979a, b; McPherson and Vangeison 1975). However, the effects of temperature on development and reproduction have not been investigated. Thus, the present study was conducted to determine the effects of 3 temperatures on these parameters. Also, notes were taken on the precopulatory and copulatory behaviors.

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MATERIALS AND METHODS

E. t. tristigmus adults were collected during June 1979 from common mullein, *Verbascum thapsus* Linnaeus, in Jackson Co., Illinois. They were placed in mason jars (5 males and 5 females per jar) and held in incubators maintained at 27 ± 1.2°C and a 16L:8D photoperiod. The mason jars were furnished with paper toweling and filter paper for absorption of excrement and additional walking surface, and green snap beans, *Phaseolus vulgaris* Linnaeus, for food, as described by McPherson (1971). All experiments described below used mason jars prepared similarly to those for maintaining field-collected adults. Cheesecloth was provided as an oviposition site for these adults and for those in subsequent experiments. Incubator temperatures (given below without ranges) were 22 ± 1.3, 27 ± 1.2 and 32 ± 1.9°C.

Effects of Temperature on Development Rate

Forty male and 40 female P_1 adults were selected from the offspring of field-collected adults, placed in mason jars (5 of each sex/jar), and maintained at 27°C in a 16L:8D photoperiod. Cheescloth with attached egg clusters was removed daily and placed on moist filter paper in petri dishes (ca. 9 cm. diam., 2 cm. deep). The dishes were placed in a 16L:8D photoperiod at 22, 27 or 32°C. The 1st instars (a nonfeeding stage) were also kept in the dishes. Distilled water was added every 1-3 days to maintain high humidity. The 2nd through 5th instars were reared to adults in mason jars at the same temperature as the eggs and 1sts. Each jar contained nymphs that had hatched from the same egg cluster. The lengths of stadia were determined for all instars by recording daily the number of exuviae. Stadia were statistically compared within and between the 3 developmental temperatures.

Effects of Temperature on Reproduction

Twenty F_1 generation male and female adults were selected from each of the 3 developmental temperatures (22, 27, 32°C) and isolated by pairs in mason jars in their respective temperatures; these were later supplemented with additional pairs as mortality among the original pairs occurred. Of these, 18, 25 and 14 pairs survived and reproduced in 22, 27 and 32°C, respectively. The resulting egg clusters were placed in petri dishes, as described above, and incubated until hatching; these eggs provided data on fecundity, fertility and hatch per female. Fecundity was defined as the number of eggs laid, fertility as the percent of eggs that developed eye spots, and hatch as the percent of eggs laid (and percent of fertile eggs laid) that successfully completed development. Also recorded were the preoviposition, oviposition and postoviposition periods. The preoviposition period was the time between the final molt (adulthood) and the 1st oviposition, the oviposition period the time between the 1st and final ovipositions, and the postovipostion period the time between the final oviposition and death.

Most comparisons of temperature effects on reproduction were based only on data collected during the 1st, 12, 12 and 8 weeks of oviposition period at 22, 27, and 32°C, respectively, the length of time being determined by the rate of mortality. Data collected beyond these periods were statistically weak since the numbers of surviving females were low.

Total fecundity, fertility and hatch, and the lengths of the preoviposition, oviposition and postoviposition periods, were compared between temperatures; fecundity, fertility and hatch were also compared between weeks within each temperature. Also, since lengths of oviposition periods varied within each temperature, each period was divided into quarters, and the fecundities compared, to determine if the rate of fecundity changed in each temperature during the oviposition period. Finally, the daily rates of fecundity in the 3 temperatures were compared.

Reproductive Behavior

Ten male and 10 female F_1 adults were separated by sex and maintained in 2 mason jars at 27°C and a 16L:8D photoperiod. A minimum of 3 weeks was allowed for maturation of the reproductive systems. Subsequently, a male and female were placed in a petri dish and observed for mating behavior. If copulation occurred within 30 minutes, the pair (still within the dish) was returned to the incubator and checked 3-5 times per day until copulation ended (usually within 2 days). Otherwise, each animal was returned to its respective mason jar and a new pair selected for observation. Ten pairs were observed during this study, 6 of which exhibited precopulatory and copulatory behaviors.

Statistics

Data that consisted of counts (e.g., fecundity) were analyzed with the χ^2 one-sample test (Siegel 1956), and the remaining data (e.g., developmental rate) with Kramer's extension of the multiple range test for unequal sample sizes (Kramer 1956). The 0.01 level of significance was chosen because of high individual variation between animals.

RESULTS AND DISCUSSION

Effects of Temperature on Developmental Rate

Lengths of the egg, 1st and 2nd stadia were longest at 22 and shortest at 32°C (Table 1). The 3rd, 4th and 5th stadia were longest at 22 but shortest at 27°C, supporting the conclusion of Davidson (1944) that harmful effects of high temperatures are greater in the more advanced stages of the life cycle. The total developmental period from egg to adult averaged 50.56, 33.62 and 35.13 days at 22, 27 and 32°C, respectively. The above results suggest that the optimal temperature for total development is between 27 and 32°C.

The 1st and 5th stadia were shorter and longer, respectively, within each temperature than the remaining stadia (Table 1); these results agree with the findings of McPherson (1971) who reared this insect at 23.9°C. No other patterns within or between temperatures were found.

Effects of Temperature on Reproduction

Fecundity

Egg cluster sizes averaged 16.4, 12.9 and 7.8 eggs at 22, 27 and 32°C, respectively, and were significantly different from each other (22 vs. 27°C, $\chi^2 = 222.4$; 27 vs. 32°C, $\chi^2 = 206.8$). Fourteen was the most frequent cluster size and represented 29.4, 37.7 and 19.7% of the clusters laid at 22, 27 and 32°C, respectively (Fig. 1A-C).

Mean cluster size at 27°C did not change over time during the recorded oviposition period (Table 2). Mean cluster size at 22°C was generally smaller during weeks 7-12 of the oviposition period, particularly during weeks 10-12. The number of clusters laid after 5 weeks by 32°C females was insufficient for statistical analysis. However, during the 5 weeks, mean cluster size changed over time and was smallest during weeks 1-2, and largest during week 3.

Total fecundities averaged 374.5, 219.2 and 67.6 at 22, 27 and 32°C, respectively, and were significantly different from each other (Table 3).

To determine if the differences in total fecundity between temperatures were due to different rates of fecundity and/or different lengths of oviposition periods, both were compared between temperatures. Rate of fecundity for each temperature (listed in Table 4) was calculated as a mean daily rate by dividing the total fecundity for that temperature by the corresponding total of the oviposition period length. However, the actual χ^2 comparisons between temperatures were made using observed and expected total fecundities for each temperature.

The results show that rate of fecundity was highest at 22, and lowest at 32°C (Table 4). Also, the oviposition period was longest at 22, and shortest at 32°C (Table 9). These results clearly explain the differences in fecundity between the 3 temperatures.

Weekly fecundities at 22 and 27°C showed no consistent pattern during the 1st 12 weeks of oviposition (Table 5). However, fecundities were generally lower during weeks 7-12, and particularly during weeks 10-12. Fecundities at 32°C showed a similar pattern over time to those

Table 1. Comparison of the effects of temperature on lengths (in days) of developmental stadia of *E. t. tristigmus.*[1]

	Temperature (°C)					
		22		27		32
Instar	N	Stadium[2,3]	N	Stadium[2,3]	N	Stadium[2,3]
Egg	759	8.50 ± 0.03[a]	828	5.37 ± 0.02[a]	787	4.01 ± 0.01[a]
Nymph						
1st	610	4.99 ± 0.04[b]	716	3.03 ± 0.01[b]	685	2.69 ± 0.02[b]
2nd	245	8.37 ± 0.08[a]	279	6.03 ± 0.09[c]	368	5.24 ± 0.08[c]
3rd	228	7.49 ± 0.07[c]	270	5.34 ± 0.10[d]	277	6.26 ± 0.14[d]
4th	220	8.54 ± 0.09[a]	262	5.72 ± 0.10[e]	226	7.19 ± 0.17[e]
5th	199	12.67 ± 0.15[d]	242	8.13 ± 0.10[f]	196	9.74 ± 0.27[f]

[1]All comparisons within stadia between temperatures (not shown here) were significantly different at the 0.01 level of probability by Kramer's extension of the multiple range test for unequal sample sizes.
[2]Stadia within temperatures followed by the same letter are not significantly different at the 0.01 level of probability by Kramer's extension of the multiple range test for unequal sample sizes.
[3] $\bar{X} \pm SE$.

of 22 and 27°C, but this pattern was limited to 8 weeks (e.g., fecundities during weeks 5-8 were lower than during weeks 1-4).

Comparison of fecundity between quarters of the 1st 12 weeks of oviposition showed that females at 22°C laid fewer eggs during the last quarter than during the first 3, those at 27°C progressively fewer eggs during the first 3 quarters, and those at 32°C fewer eggs during the last 2 quarters (Table 6).

Fertility

Total egg fertilities averaged 77.4, 76.7 and 24.0% at 22, 27 and 32°C, respectively; those at 22 and 27°C were nonsignificantly different, and were higher than that at 32°C (Table 3).

Fertility over time showed no pattern of change at 22°C and, in fact, was slightly higher during weeks 7-12 of the recorded oviposition period (Table 7); this increase was probably due to random variation. Fertilities in 27 and 32°C remained constant throughout the oviposition periods.

Hatch

Total percent hatches of eggs laid averaged 70.2, 65.0 and 20.3% at 22, 27 and 32°C, respectively, and were significantly different from each other (Table 3). Total percent hatches of fertile eggs averaged 90.7, 84.7 and 84.6% at 22, 27 and 32°C, respectively; that at 22°C was highest while those at 27 and 32°C were nonsignificantly different from each other (Table 3).

Percent hatch over time showed no pattern of change at 22°C and, similar to fertility, variation was probably random (Table 8). Percent hatch at 27°C did not change over time, while that at 32°C was higher during the last 3 weeks of the recorded oviposition period. We have no explanation for the increase at 32°C.

Preoviposition Period

The preoviposition periods averaged 19.6, 15.0 and 20.8 days at 22, 27 and 32°C, respectively, but were nonsignificantly different from each other (Table 9).

Oviposition Period

The oviposition periods averaged 77.8, 46.3 and 23.5 days at 22, 27 and 32°C, respectively, and were significantly different from each other (Table 9). As noted earlier, the 22°C females had

Table 2. Comparison of the effects of temperature on egg cluster size per week of *E.t. tristigmus*.

Temp. (°C)	Week	No. of Clusters	Eggs per Cluster[3]	Temp. (°C)	Week[2]	No. of Clusters	Eggs per Cluster[3]	χ^2 of weeks compared[1] 22°	22°	32°
22	1	53	15.0 ± 1.3	27	1	101	13.3 ± 0.7			
	2	35	15.4 ± 1.5		2	58	12.2 ± 0.8			
	3	32	18.2 ± 1.6		3	46	12.5 ± 0.9			
	4	35	19.0 ± 1.2		4	51	14.2 ± 0.7			
	5	36	17.6 ± 1.0		5	50	12.6 ± 0.8			
	6	32	17.1 ± 1.5		6	36	12.5 ± 1.1			
	7	42	17.6 ± 1.4		7	21	12.1 ± 0.9			
	8	30	17.4 ± 1.3		8	23	11.7 ± 1.6			
	9	33	14.1 ± 1.3		9	13	11.8 ± 1.1			
	10	26	15.9 ± 1.4		10	16	13.9 ± 2.0			
	11	31	13.8 ± 1.5		11	8	12.4 ± 2.6			
	12	13	13.4 ± 1.8		12	— —	— —			
	1-12							75.4*		
	1-6 vs. 7-12							15.5*		
	7-9 vs. 10-12							10.0*		
	1-11								17.1	
32	1	40	6.3 ± 0.8							
	2	36	6.8 ± 1.1							
	3	19	11.6 ± 1.3							
	4	13	9.4 ± 1.3							
	5	10	7.8 ± 2.2							
	6	— —	— —							
	7	— —	— —							
	8	— —	— —							
	1-5									54.4*
	1-2 vs. 3-5									41.0*
	3 vs. 4-5									8.6*

*Significant at the 0.01 level of probability. [1]Comparisons were made between total egg counts, not means.
[2]Dashed line = insufficient data collected during corresponding week for inclusion in the statistical analyses. [3]$\overline{X} \pm SE$.

the highest total fecundity of the 3 groups (i.e., 22, 27 and 32°C females) and this is explained by their having the highest rate of fecundity and longest oviposition period.

Postoviposition Period

The postoviposition periods averaged 5.3, 7.4 and 12.6 days at 22, 27 and 32°C, respectively, but were nonsignificantly different from each other (Table 9).

Adult Lifespan

The total of the 3 periods (i.e., preoviposition, oviposition and postoviposition) averaged 102.9, 64.1 and 52.4 days at 22, 27 and 32°C, respectively; those at 27 and 32°C were nonsignificantly different and were shorter than that at 22°C (Table 9).

Table 3. Comparison of the effects of temperature on total fecundity, egg fertility and hatch of *E. t. tristigmus.*

Parameter	Temp. (°C)	No. of Females	$\overline{X} \pm SE$	χ^2 of temps. compared[1] 22 vs. 27 vs. 32	22 vs. 27	27 vs. 32
Fecundity	22	18	374.5±29.0			
	27	25	219.2±22.3			
	32	14	67.6±17.2	3239.6*	888.4*	1251.6*
Fertility (%)	22	18	77.4±7.4			
	27	25	76.7±5.2			
	32	14	24.0±8.6	983. 5*	0.1	324.8*
Hatch (%) of eggs laid	22	18	70.2±7.9			
	27	25	65.0±6.4			
	32	14	20.3±8.0	321.2*	12.0*	276.4*
Hatch (%)of fertile eggs	22	18	90.7±6.4			
	27	25	84.7±4.1			
	32	14	84.6±12.0	9.7*	9.2*	0.0

*Significant at the 0.01 level of probability.

[1]Comparisons were made between total egg counts, not means.

Table 4. Comparison of the effects of temperature on daily fecundity (total fecundity/oviposition period) of *E. t. tristigmus.*

			χ^2 of temps. compared[2]		
Temp. (°C)	No. of Females	Daily Fecundity[1]	22 vs. 27 vs. 32	22 vs. 27	27 vs. 32
22	18	4.8±0.3			
27	25	4.6±0.4			
32	14	2.9±0.4	224.4*	9.0*	173.8*

*Significant at the 0.01 level of probability.

[1]$\overline{X} \pm SE$.

[2]Comparisons were made between total egg counts, not means.

Table 5. Comparison of the effects of temperature on fecundity per week of *E. t. tristigmus.*

Temp, (°C)	Week	No. of Females	Fecundity[2]	Temp. (°C)	Week	No. of Females	Fecundity[2]	χ^2 of weeks compared[1] 22°	27°	32°
22	1	18	44.3 ± 4.7	27	1	25	54.4 ± 4.3			
	2	18	30.0 ± 4.0		2	24	30.0 ± 3.4			
	3	18	32.3 ± 5.3		3	24	24.5 ± 3.4			
	4	18	37.0 ± 3.9		4	21	33.9 ± 4.7			
	5	18	35.2 ± 3.9		5	21	30.0 ± 3.5			
	6	18	30.3 ± 4.6		6	19	23.7 ± 3.1			
	7	17	43.6 ± 3.6		7	16	16.7 ± 3.2			
	8	17	30.7 ± 4.2		8	13	20.3 ± 4.8			
	9	17	27.3 ± 4.4		9	12	13.8 ± 4.2			
	10	17	24.3 ± 4.7		10	10	21.6 ± 7.8			
	11	14	30.6 ± 4.8		11	9	9.3 ± 4.9			
	12	12	14.5 ± 4.2		12	6	4.7 ± 4.7			
	1-12							332.4*	1136.0*	
	1-6 vs. 7-12							55.4*	515.3*	
	7-9 vs. 10-12							120.3*	13.6*	
32	1	14	18.1 ± 4.0							
	2	14	17.5 ± 4.9							
	3	13	16.9 ± 5.4							
	4	10	12.2 ± 4.7							
	5	8	9.7 ± 3.6							
	6	8	0.6 ± 0.6							
	7	5	2.8 ± 2.8							
	8	3	0.3 ± 0 3							
	1-8									250.2*
	1-4 vs. 5-8									199.7*
	5-6 vs. 7-8									14.4*

*Significant at the 0.01 level of probability.
[1]Comparisons were made between total egg counts, not means. [2]$\overline{X} \pm SE$.

Table 6. Comparison of the effects of temperature on fecundity per quarter of oviposition period of *E. t. tristigmus.*

Temp (°C)	Quarter	No. of Females	Fecundity[2]	Temp. (°C)	Quarter	No. of Females	Fecundity[2]	χ^2 of quarters compared[1]		
								22°	27°	32°
22	1	18	103.7 ± 10.2	27	1	24	80.5 ± 8.6			
	2	18	97.7 ± 8.2		2	24	55.9 ± 8.3			
	3	18	98.9 ± 9.8		3	24	43.4 ± 4.6			
	4	18	75.6 ± 6.9		4	24	47.7 ± 6.0			
	1	12	25.7 ± 5.7							
	2	12	24.5 ± 7.3							
	3	12	13.4 ± 4.5							
	4	12	13.8 ± 3.8							
	1-4							90.3*	347.2*	81.6*
	1 vs. 2							3.2	106.8*	0.3
	2 vs. 3							0.1	37.7*	38.9*
	3 vs. 4							55.9*	4.7	0.1

*Significant at the 0.01 level of probability.
[1] Comparisons were made between total egg counts, not means.
[2] $\overline{X} \pm SE$.

Conclusions

The above results shows that although the optimal temperature for development of immatures appears to be between 27 and 32°C, those for high fecundity and a long oviposition period appear to be closer to 22°C. High temperature (i.e., 32°C) adversely affects fecundity, fertility, hatch and length of the oviposition period.

Reproductive Behavior

Precopulatory and copulatory behaviors were observed between 6 pairs of animals. Courtship was initiated by the male who usually began by antennating the female's antennae, but sometimes her head, thorax or abdomen. Contacts between the 2 were often sporadic at first but became more numerous. The male then moved to the female's side, antennating more rapidly than before. He occasionally moved back to her head or to her opposite side. Often there were long pauses during this period and sometimes one individual walked away from the other.

If the male continued antennating, either he would move to the end of the female's abdomen or she would turn her abdomen toward him. By this time, she usually had slightly elevated her abdomen. He then vigorously antennated her abdominal venter and she, if receptive, responded by lifting her abdomen usually 45 to 60° above the substrate. If he stopped antennating, she often lowered her abdomen. Throughout this period the male's abdomen vibrated up and down a short distance. His antennating of her venter lasted from a few seconds to ca. 3 minutes.

Next, the male extended and rotated his aedeagus 180° just before or as he turned 180°. He then lifted his abdomen to reach hers, and sometimes needed to twist the genital cup into place to initiate copulation. Sometimes he pushed at the end of her abdomen with his hind legs just after inserting his aedeagus.

Table 7. Comparison of the effects of temperature on egg fertility per week of *E. t. tristigmus.*

Temp. (°C)	Week[2]	No. of Females	Percent Fertility[3]	Temp. (°C)	Week[2]	No. of Females	Percent Fertility[3]	χ^2 of weeks compared[1] 22°	27°	32°
22	1	18	67.5 ± 9.8	27	1	25	71.6 ± 6.9			
	2	15	86.7 ± 5.7		2	24	68.7 ± 7.8			
	3	17	82.1 ± 7.8		3	21	78.8 ± 6.5			
	4	17	75.9 ± 7.0		4	19	81.3 ± 5.6			
	5	16	93.6 ± 6.5		5	20	82.9 ± 5.0			
	6	15	76.9 ± 8.2		6	17	78.7 ± 5.5			
	7	17	83.8 ± 8.5		7	12	81.7 ± 5.1			
	8	15	83.1 ± 7.2		8	11	83.9 ± 6.2			
	9	13	87.9 ± 7.4		9	8	84.1 ± 7.6			
	10	12	72.6 ± 8.7		10	7	69.9 ± 11.4			
	11	12	76.6 ± 8.4		11	3	82.2 ± 11.2			
	12	7	88.0 ± 9.1		12	— —	— —			
	1-12							55.6*		
	1-6 vs. 7-12							9.6*		
	7-9 vs. 10-12							4.6		
	1-11								22.1	
32	1	14	18.6 ± 9.4							
	2	12	22.4 ± 10.4							
	3	10	26.5 ± 11.4							
	4	5	34.6 ± 18.3							
	5	5	23.1 ± 19.3							
	6	— —	— —							
	7	— —	— —							
	8	— —	— —							
	1-5									9.7

*Significant at the 0.01 level of probability.
[1]Comparisons were made between total egg counts, not means.
[2]Dashed line = insufficient data collected during corresponding week for inclusion in the statistical analyses.
[3]$\overline{X} \pm SE$.

Table 8. Comparison of the effects of temperature on egg hatch (% of total eggs laid) per week of *E. t. tristigmus*.

Temp. (°C)	Week[2]	No. of Females	Percent Hatch[3]	Temp. (°C)	Week[2]	No. of Females	Percent Hatch[3]	χ^2 of weeks compared[1]		
								22°	27°	32°
22	1	18	63.5 ± 9.4	27	1	25	63.0 ± 7.4			
	2	15	78.9 ± 7.4		2	24	60.7 ± 8.4			
	3	17	69.3 ± 8.8		3	21	66.9 ± 7.3			
	4	17	70.9 ± 7.2		4	19	69.8 ± 8.0			
	5	16	79.8 ± 7.5		5	20	67.0 ± 7.9			
	6	15	71.3 ± 9.1		6	17	64.3 ± 8.6			
	7	17	72.0 ± 8.5		7	12	67.6 ± 8.5			
	8	15	74.0 ± 8.0		8	11	71.1 ± 10.0			
	9	13	78.9 ± 8.0		9	8	69.5 ± 12.6			
	10	12	73.6 ± 9.2		10	7	60.8 ± 14.5			
	11	12	67.4 ± 9.9		11	3	67.7 ± 20.1			
	12	7	78.7 ± 12.2		12	– –	– –			
	1-12							29.0*		
	1-6 vs. 7-12							5.6		
	7-9 vs. 10-12							4.8		
	1-11								19.9	
32	1	14	16.0 ± 8.5							
	2	12	18.7 ± 10.1							
	3	10	25.4 ± 11.4							
	4	5	32.7 ± 18.3							
	5	5	22.2 ± 18.6							
	6	– –	– –							
	7	– –	– –							
	8	– –	– –							
	1-5									14.8*
	1-2 vs. 3-5									164.8*

*Significant at the 0.01 level of probability.

[1] Comparisons were made between total egg counts, not means.

[2] Dashed line = insufficient data collected during corresponding week for inclusion in the statistical analyses.

[3] $\bar{X}$ ± SE.

Table 9. Comparison of the effects of temperature on lengths (in days) of preoviposition, oviposition and postoviposition periods of *E. t. tristigmus.* [1]

	Temperature (°C)					
	22°		27°		32°	
Period	No. of Females	Period Length[2]	No. of Females	Period Length[2]	No. of Females	Period Length[2]
Preoviposition	19	19.6 ± 1.0[a]	23	15.0 ± 0.8[a]	14	20.8 ± 2.6[a]
Oviposition[3]	18	77.8 ± 4.4[a]	26	46.3 ± 4.9[b]	14	23.5 ± 4.6[c]
Postoviposition	18	5.3 ± 1.5[a]	25	7.4 ± 1.6[a]	14	12.6 ± 3.0[a]
Total	18	102.9 ± 4.8[a]	22	64.1 ± 5.1[b]	14	52.4 ± 4.9[b]

[1]Means within periods between temperatures followed by the same letter are not significantly different at the 0.01 level of probability by Kramer's extension of the multiple range rest for unequal sample sizes.

[2]$\bar{X} \pm SE$.

[3]Oviposition period based on total length of period per female, not just the first 12 weeks of oviposition.

If the male failed to insert, he usually turned back around and antennated the female's abdomen for ca. 10 to 30 seconds before again extending his aedeagus and attempting copulation. One male attempted to copulate 6 times before he was successful.

During copulation, the male often rested his hind tarsi on the female's hind legs or abdomen. The angle of their bodies with the substrate decreased from ca. 45 to near 0° (horizontal) within 1 to a few hours after copulation began. The pair did not remain stationary during copulation but moved about, the direction usually being controlled by the female. Copulation last from less than 36 to 48 hours or more, and both sexes fed during this time.

Two of the males vibrated from side to side for about 1 second, 2 to 3 times during courtship. One male, while vibrating, partially extended his aedeagus. Fish and Alcock (1973) reported that in *Chlorochroa ligata* (Say), a male will rapidly jerk his body while attempting to lift the female's abdomen with his head. Both sexes of *Brochymena quadripustulata* (Fabricius) jerk their bodies from side to side shortly after beginning copulation (Cuda and McPherson 1976, Gamboa and Alcock 1973). It would be interesting to know if the jerking motions observed in these 3 species are related, even though they occurr at different times during their mating behaviors.

No *E. t. tristigmus* male, during precopulation, even attempted to lift the female's abdomen with his head; this has also been reported for male *Murgantia histrionica* (Hahn) (Lanigan and Barrows 1977). However, it appears from the literature that lifting the female's abdomen in this manner is usually part of the male's precopulatory behavior (Alcock 1971, Cuda and McPherson 1976, Fish and Alcock 1973, Gamboa and Alcock 1973, Mitchell and Mau 1969, Vangeison and McPherson 1975, Youther and McPherson 1975).

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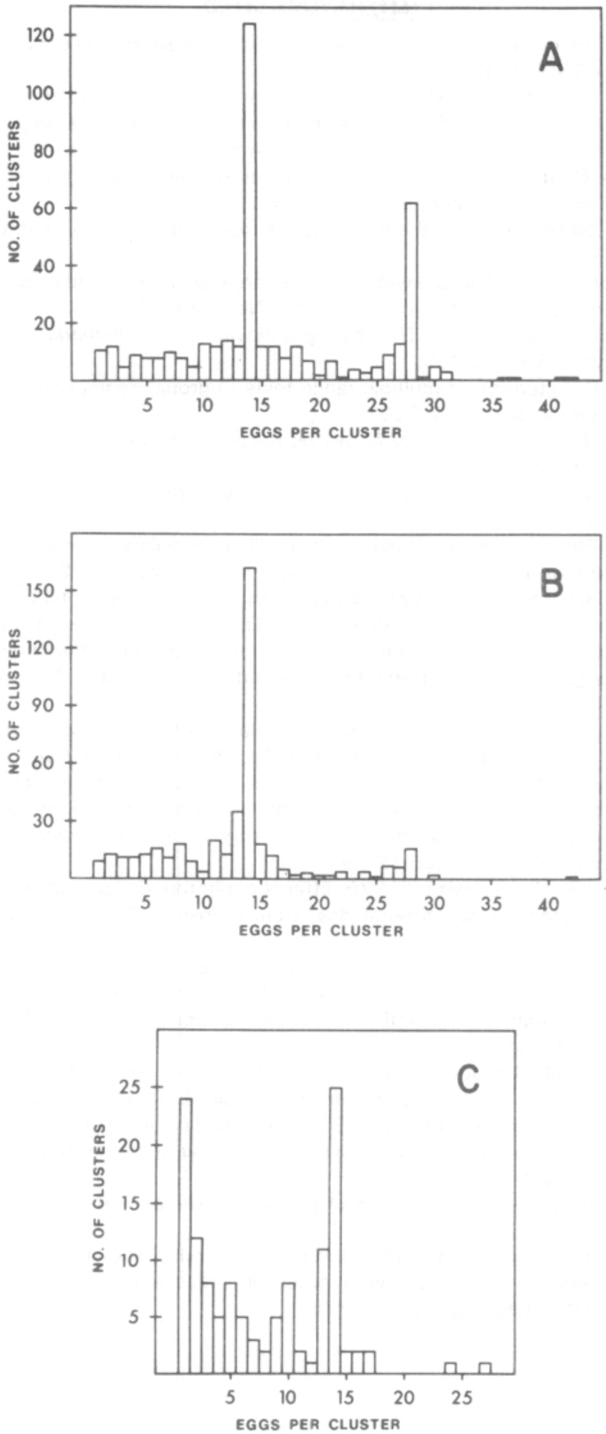

Fig. 1. Frequency distribution of egg cluster sizes of *E. t. tristigmus* at 22(A), 27(B) and 32(C)°C.

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