REPRODUCTIVE BIONOMICS OF THE SQUASH BUG,

Anasa tristis (HETEROPTERA: COREIDAE)

AS AFFECTED BY TEMPERATURE

By

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Finally, I dedicate this work to my late Mother who gave me life.

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LIST OF SYMBOLS

avg	average
C	centigrade
ca	approximately
cm	centimeter
d	day
f_i	number of eggs developing
h	hour
i	ith observation treatment
y	mean of ith treatment
mm	millimeter
n	number
obs	observation
ovip	oviposition phase
prem	premating phase
preov	preoviposition phase
rh	relative humidity
sensc	senescent phase
s.e.	standard error
temp	temperature
wk	week
y_i	development time

CHAPTER I

INTRODUCTION

The squash bug, Anasa tristis DeGeer (Heteroptera: Coreidae) occurs throughout the western hemisphere from South America northward into Canada. A. tristis is found throughout the United States, and is particularly abundant east of the Rocky Mountains, ranging from Maine to the Gulf States (Wadley, 1920; Elliott, 1935; Beard, 1940).

A. tristis is a serious pest of cucurbits and may cause severe economic damage to cucurbit production. All life stages of the insect damage the plant by removing fluids. Squash plants show localized leaf damage and eventually die if squash bug populations reach high densities (Britton, 1919; Beard, 1935 and 1940).

Adult squash bugs overwinter under debris of various types, in crevices, or between boards of buildings (Beard, 1940). During May-June the overwintered adults invade the field, begin to mate and oviposit. In Oklahoma, oviposition continues until August or early September (Fargo, et al., 1987). During the early season (May-June) squash bug damage is concentrated on the leaves. Damaged leaves wilt and die causing a decrease in photosynthetic area thereby reducing total fruit production (Beard, 1940; Resner, 1985).

Squash bug egg masses are generally laid on the lower leaf surface of squash plants with a mean number of 19.5 $\pm$ S.D. 3.96 eggs per mass (Bonjour and Fargo, unpublished). Oviposition peaks in early July in northern climates but continues to increase throughout the summer in the South (Fargo, et al., 1987). Eggs hatch within five to twelve days, depending on temperature (Fargo and Bonjour, 1987). The squash bug passes through five nymphal instars prior to becoming an adult (Chittenden 1908; Elliott, 1935; Beard, 1940).

Published literature is primarily devoted to A. tristis control (Hoerner, 1938; Criswell, 1985). Several workers including Wadley (1920), Beard (1940), and more recently Nechols (1987) and Fargo, et al. (1987) have described various aspects of the insect's bionomics. Very little is known, however, regarding the reproductive behavior of A. tristis and how this behavior may be affected by temperature.

The objectives of this investigation were to determine the effect of different constant temperatures on 1) adult longevity, 2) reproductive cycle, 3) fecundity, 4) egg viability, and 5) egg development of A. tristis.

CHAPTER II

LITERATURE REVIEW

General Biology

The squash bug attacks all plants in the cucurbit family (Cucurbitales: Cucurbitaceae). It was first described by DeGeer in 1773 under the name Cimax tristis and it has been found wherever cucurbits are grown in North America (Elliot, 1935; Beard, 1940). Overwintered squash bugs attack plants soon after the insect's emergence, which may vary from early spring in the south to late June in the extreme north (Chittenden, 1908). The squash bug prefers squash and pumpkin (Balduf, 1950; Bonjour and Fargo, unpublished), however, it is also found on other cucurbit cultivars such as cucumber and melon.

The adult squash bug varies from 13.0 to 16.5 mm in length and from 4.5 to 6.0 mm in width (Wadley, 1920; Beard, 1940). Balduf (1950) noted that average female size exceeded that of the male by 1.39 mm. He also noted that the size of the adult squash bug diminished gradually as food availability decreased.

Numerous papers have reported the effect of temperature on various insects. However, the majority of publications on the squash bug deal with life history and bionomics (Chittenden, 1899; Chittenden, 1908, Britton, 1919; Wadley, 1920; Worthley, 1923; Beard, 1935; Elliot, 1935; Haseman, 1937; Beard, 1940; Nechols, 1987; and Fargo, et al., 1987). They state that temperature influences oviposition, bionomics, and rate of development. Each aspect of the reproductive bionomics of A. tristis will be addressed separately in this study. Information available for A. tristis will be reported with additional support using data from insects in related groups.

Longevity

Beard (1940) reported that mated female A. tristis lived significantly longer when kept separated from males (81 vs. 43 days). Carrol and Wangberg (1981) found that the longevity of cactus bugs, Chelinidea vittiger Uhler (Heteroptera: Coreidae), was inversely related to temperature. Kehat and Wyndham (1974) found that Nysius vinitor Bergroth (Heteroptera: Lygaeidae) adults lived longer at a continuous low temperature than any other stage, but were susceptible to high temperatures. Mueller and Stern (1973) reported no significant difference in longevity between females of Lygus hesperus Knight and L. elisus Van Duzee (Heteroptera: Miridae) at 26.7°C with a 14:10 light/dark photoperiod. However, L. hesperus females lived significantly longer than L. elisus females at 20°C with a 12.5:11.5 light/dark photoperiod. Strong and Sheldahl (1970) demonstrated that at 12.8°C, mean female longevity of L. hesperus was 120 days with a maximum longevity of 200 days. Longevity decreased as temperature increased.

Fecundity

Generally, the reproductive activity of adult squash bugs is limited by weather conditions (temperature, humidity, and daylight). However, specific information on the influence of temperature on A. tristis is not available. Oviposition by A. tristis is believed to be favored by higher temperatures and decreased with the onset of cool weather (Beard, 1935 and 1940; Fargo, et al., 1987). Eggs are usually deposited in regular rows which may be closely crowded together or widely separated. Egg masses are usually deposited on the lower surface of squash leaves, but may also occur on the upper leaf surface and on the stems (Bonjour and Fargo, unpublished). When laid on the lower leaf surface between two veins, the egg mass remains compact. Average egg mass size is given by various authors as: 15, 15.4, 16.9, 14.2, and 19.5 eggs per mass (Wadley, 1920; Beard, 1935; Elliot, 1935; Beard, 1940; and Bonjour and Fargo, unpublished, respectively). Total egg production per female has been reported as 150 (Girault, 1904), 356 (Wadley, 1920), and 409 eggs (Beard, 1940). Squash bugs lay an average of ten eggs per day (Wadley, 1920; Beard, 1940). Elliot (1935) found that the squash bug deposited 92% of its eggs between 0800 and 1700 hours, and that egg-laying extended over a period of six to seven weeks.

The number of eggs deposited by A. tristis is limited more by environmental conditions than by the number of cells contained in the insect ovary. Beard (1940) reported that the number of ovaries did not affect the potential to lay a full complement of eggs. This is because the insect was able to compensate for the loss in the number of ovaries. He also found that the seasonal changes had a great influence on total fecundity. Beard (1940) reported that multiple matings were not essential for continuous deposition of eggs by A. tristis. Females which were allowed to mate only once and then placed in individual cages laid more eggs than females remaining with males.

Although limited studies exist describing the influence of temperature on ovipositional activity of the squash bug, several workers have described the influence of temperature on ovipositional activity of the other hemipterous insects with close taxonomic affinity to A. tristis. Carrol and Wangberg (1981) reported that cactus bugs, Chelinidea vittiger Uhler (Heteroptera: Coreidae), produced the maximum number of eggs at 38°C. However, at 31°C there was a higher percentage of ovipositing females, with the highest cumulative mean number of eggs.

Suzuki, et al. (1979) studied oviposition of overwintering adults of Cavelerius saccharivorus Okajima (Heteroptera: Lygaeidae) at five constant temperature regimes: 10, 15, 20, 25, and 27°C. Oviposition by C. saccharivorus increased with temperature; no eggs were laid at 10°C. Mean egg mass size was not significantly different among the various temperatures.

Dunbar and Bacon (1972) examined the reproduction of Geocoris atricolor Montandon (Heteroptera: Lygaeidae), G. pallens Stal, and G. punctipes oviposited at 23.9°C but not at 35.0°C.

Clair and McPherson (1980) studied the effect of three constant temperatures (22, 27, and 32°C) on reproduction of Euschistus tristigmus (Say) (Heteroptera: Pentatomidae). Fecundity was the highest at 22°C but decreased at 32°C. Fecundities were significantly different among the three temperatures. Also, the oviposition period was longest at 22°C and shortest at 32°C. Weekly fecundities at 22 and 27°C showed no consistent pattern during the first 12 weeks of oviposition. Fecundity was generally lower during weeks 7-12, particularly during weeks 10-12. Fecundity at 32°C showed a similar pattern, but was limited to 8 weeks.

Lygus hesperus Knight and Lygus elisus Van Duzee (Heteroptera: Miridae) were studied under two constant temperature regimes by Mueller and Stern (1973). Preoviposition periods at 26.7 and 20°C were not significantly different in either species. L. hesperus females laid an average of 161.6 eggs and 117.3 eggs at 26.7 and 20°C, respectively, while L. elisus oviposited only 47.7 and 38.2 eggs per female at 26.7 and 20°C, respectively.

Strong and Sheldahl (1970) reported that the mean number of eggs per female increased with a temperature increase from 12.8 to 26.7°C. However, egg production started to decline when the temperature was increased to 32.3°C with no eggs being produced at 37.8°C. Maximum egg production at a constant temperature occurred at 26.7°C, however the overall maximum egg production occurred in the 12.8 to 26.7°C fluctuating temperature regime.

Egg Viability

Egg viability is the percentage of eggs which eclose. Little information about the temperature effect on egg viability of A. tristis has been reported although Elliot (1935) and Beard (1940) found that viability of A. tristis eggs was very high and averaged 96% at 23.3°C. Champlain and Sholdt (1967) studied egg viability of the bigeyed bug, Geocoris punctipes (Say) (Heteropetera: Lygaeidae), at several constant temperatures and found that eggs hatched at 15°C but that the nymphs failed to develop into adults. They also found that a temperature of 40°C was lethal to eggs. Egg viability in G. atricolor and G. pallens was high between 23.9-35.0°C while viability in G. punctipes was high between 23.9-32.2°C (Dunbar and Bacon, 1972).

Clair and McPherson (1980) reported that egg viability of the pentatomid Euschistus tristigmus (Say) was highest at 22°C and lowest at 32°C. Eguagie (1972) found that the egg viability of Tingis ampliate H.-S. (Heteroptera: Tingidae) increased with increasing temperatures in the range 15-30°C, but viability at 25°C was not significantly different from that at 30°C and no eggs hatched at 10°C.

Khattat and Stewart (1977) found that within the average of 20-28°C constant temperature, the percent of eggs which hatched decreased with increasing temperature.

Egg Development

Elliot (1935) reported that the duration of the egg stage of A. tristis varies with temperature. During hot weather development time varied from 7 to 9 days while in cold weather it ranged from 10-17 days. Beard (1940) reported that the duration of A. tristis egg development varied from 7-17 days under field conditions and that development was dependent on location and temperature. More recently, Fargo, et al. (1987) showed that egg development times for A. tristis decreased with increasing temperature from 18 days at 20°C to 6.4 days at 33.3°C. No eclosion occurred at 15.6 or above 33.3°C.

Champlain and Sholdt (1966) reported that the duration of egg stage decreased as temperature increased in G. punctipes (Say). Isenhour and Yeargan (1981) found that egg development decreased significantly with each increase in temperature for the anthocorid Orius insidious (Say). Similarly, Butler and Wardecker (1971) reported that development of Lygus hesperus Knight egg development decreased with increasing temperature.

CHAPTER III

MATERIALS AND METHODS

A preliminary experiment was conducted in the laboratory to select the most suitable sustrate for oviposition by the squash bug. Seedling squash plants, sectioned squash fruit, half of a fruit, and cheese cloth were tested. This experiment was conducted in a growth chamber at 26.7 $\pm$ 1°C ca. 50% relative humidity (RH). Two replications of each treatment were used. Results indicated that over 31 days the squash bug laid significantly more eggs on the squash plants than on fruit sections, half fruits, or cheese cloth. Therefore, squash plants were used as the ovipositional substrate for this study.

Fifth instar A. tristis nymphs were collected on July 10, 1986 from the Oklahoma State University Horticulture Research Station near Perkins, Payne County, Oklahoma. Nymphs were placed on fresh squash fruit in two cylindrical cages (18 X 21 cm). Fresh fruit were provided daily. Cages were maintained in a growth chamber at 26.7°C at ca. 50% RH at the Entomology Research Laboratory, Oklahoma Agricultural Experiment Station, Stillwater, Oklahoma. When the nymphs became adults they were sexed and placed in separate cages.

This culture of A. tristis was maintained in the laboratory to initiate studies on the temperature effects on squash bug reproductive bionomics. Squash plants, Cucurbita pepo L. var. melopepo 'Yellow Straight Neck Hyrific,' were grown in the greenhouse in 5 cm square pots.

Growth chambers were maintained at 15.6, 23.3, 26.7, 31.1, and 35.6°C. These temperatures were chosen to include the minimum and maximum temperatures that normally occur during the Oklahoma growing season. A 16: 8 L:D photoperiod was utilized for each growth chamber and ca. 50% RH was maintained.

A squash plant was placed inside a cylindrical cage (18 X 21 cm) having ventilation panels on the sides and top. The bottom of each cage was covered with filter paper. A newly molted male and female A. tristis were placed in each cage. Six cages were maintained at each temperature with fresh plants supplied as necessary.

Adult longevity is defined as the number of days between adult eclosion and death. Longevity was determined in this study by continuously maintaining A. tristis adults until death.

The reproductive cycle is characterized by four distinct phases: premating, preoviposition, oviposition, and senescence. To determine the premating phase, each pair was checked five to six times daily until copulation occurred. Preoviposition was determined by the daily observation of each pair of adults until the first mass of eggs was laid. The oviposition phase of A. tristis was determined by recording the number of days that an adult female squash bug spends between the first and last oviposition. Adult female squash bugs were observed daily to determine the senescent phase which is the period from the last oviposition until death.

Fecundity is defined as the total number of eggs laid by a female during her lifetime. The number of egg masses and eggs per mass were recorded daily for each female. These observations were made between 1700-1900 hours. Although squash bugs prefer to lay eggs on the lower side of the leaf, eggs were sometimes laid on the stem and rarely on the cage surface. Leaves and stems containing eggs were collected daily and placed in petri dishes lined with filter paper. Eggs laid on the cage surface were left undisturbed and monitored for hatching. Eggs collected each week from a single female were kept in a petri dish in the associated growth chamber. Percentage of viable eggs was calculated from the eggs collected weekly. Egg development times were calculated for each temperature.

Longevity, reproductive cycle, fecundity, egg viability, and egg development were analyzed as a completely randomized design and a least significant difference (LSD) and Duncan's multiple range tests (Duncan, 1955) were used to compare means when significant differences were found.

CHAPTER IV

RESULTS AND DISCUSSION

Longevity

Mean longevity of the squash bug under five constant temperatures is summarized in Table I. There were significant differences in longevity among temperatures. Female longevity decreased as temperature increased and ranged from 171.3 days at 15.6°C to 23.2 days at 35.6°C. At 35.6°C, female longevity was significantly shorter than all other temperatures. At 31.1°C, females lived significantly longer than at 26.7°C. It was thought that a trend might occur with a steady decrease in longevity with increasing temperatures. in the present case, our results have no simple explanation. Perhaps this anomaly was due to temperature effects on insect physiology. Other unknown factors might also have influenced the physiological system which increased the female squash bug longevity. Longevity of males ranged from 193.6 days at 23.3°C to 36.0 days at 35.6°C (Table I). No significant differences ($P>0.05$) in male longevity occurred from 15.6 to 31.1°C. Male longevity at 35.6°C was significantly shorter ($P<0.05$) than at the lower temperatures.

The data in Table I show that, in general, adult longevity is inversely correlated with temperature. These data are similar to that reported for other insects. Carroll and Wangberg (1981) and Kehat and Wyndham (1974) reported that adults of Chelinidea vittiger (Uhler) and Nysius vintor Bergroth, respectively, lived longer at lower temperatures. Khattat and Stewart (1977)

TABLE I

TEMPERATURE EFFECTS ON MEAN LONGEVITY OF ADULT MALES, FEMALES, AND OVERALL LONGEVITY AT FIVE CONSTANT TEMPERATURES

Temperature °C	n	Days: Male Mean	s.d.	n	Female Mean	s.d.	n	Overall Mean	s.d.
15.6	6	187.8a	25.77	6	171.3a	5.65	12	179.6a	13.19
23.3	5	193.6a	28.23	5	139.4b	6.21	10	166.5ab	14.45
26.7	6	110.3ab	25.77	6	66.5c	5.65	12	88.4c	13.19
31.1	6	173.8a	25.77	6	91.3d	5.65	12	132.6b	14.45
35.6	5	36.0b	28.23	5	23.2e	6.21	10	29.6d	13.19

Means within a column followed by the same letter are not significantly different ($P>0.05$; Duncan's multiple range test).

found that both males and females lived significantly longer at the lower temperature regimes.

The mean longevity of adult male and female bugs was significantly different ($P<0.05$) only at 31.1°C (Figure 1). Overall, male squash bugs lived significantly longer than females when averaged over temperature ($\overline{x}$ = 141.0, and $\overline{x}$ = 99.0 days for males and females, respectively).

Reproductive Cycle

During the course of the study, aspects of the reproductive life of adult females that had been referred to only briefly in scientific literature were discovered. It was found that the reproductive cycle of the female, following adult ecdysis, consisted of four phases: premating, preovipositional, ovipositional, and senescence. These phases will be described individually.

Premating Phase

This period is defined as the time between adult female ecdysis and mating. Under laboratory conditions, the A. tristis premating phase averages 9.4, 5.3, 6.2, and 2.0 days at 23.3, 26.7, 31.1, and 35.6°C, respectively. The means at 26.7 and 31.1°C were not significantly different ($P>0.05$) (Table II), however they were significantly shorter ($P<0.05$) than the mean at 23.3°C and longer than the mean at 35.6°C. Mating squash bugs were observed earlier under higher temperatures indicating that the adults respond to warmer temperatures by earlier reproductive activity. Beard (1940) reported that an active growth takes place in the egg tubes of the female squash bug in late spring. Nechols (1987) reported that high spring temperatures cause oviposition to occur early in the season.

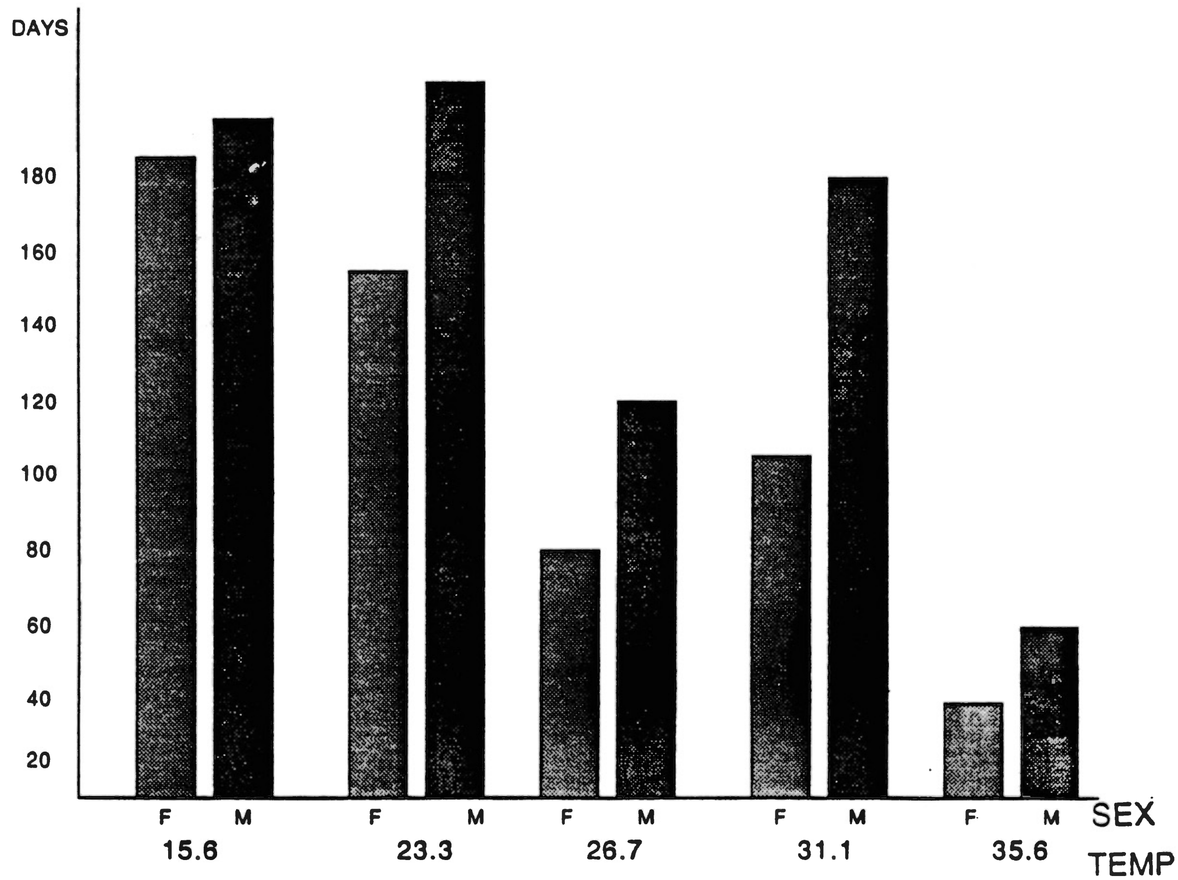

Figure1. Mean Longevity of Adult Male and Female A. tristis at Constant Temperature. Only means at 31.1°C were Significantly Different ($P<0.05$).

TABLE II

COMPARISON OF THE EFFECT OF TEMPERATURE ON LENGTHS (DAYS) OF REPRODUCTIVE LIFE CYCLE PHASES OF A. TRISTIS

Temp (^oC)	n	Prem. Mean	s.d.	Preov. Mean	s.d.	Ovip. Mean	s.d.	Senes. Mean	s.d.
15.6	6	--	--	--	--	--	--	--	--
23.3	5	9.4a	1.95	8.6a	7.40	114.8a	20.80	6.6a	5.86
26.7	6	5.3b	0.52	2.2b	1.17	53.5c	19.95	5.5a	4.32
31.1	6	6.2b	2.48	2.2b	1.17	79.3b	13.26	3.7a	1.75
35.6	5	2.0c	0.00	2.0b	1.73	14.2d	7.43	5.2a	7.19

Means within a column followed by the same letter are not significantly different ($P>0.5$; Duncan's multiple range test)

Preovipositional Phase

The preovipositional phase is defined as the number of days between initial mating and the first observation of an egg mass. The preovipositional phase averaged 8.6, 2.2, 2.2, and 2.0 days at 23.3, 26.7, 31.1, and 35.6°C, respectively (Table II). This phase was significantly ($P<0.05$) longer at 23.3°C than at the other three temperatures. Nechols (1987) reported that adult females in Kansas mate and oviposit within 3-4 days. Beard (1940) reported that for overwintered females in Connecticut, reproduction took place 5 or 6 days following adult ecdysis. Under the cooler temperatures, the preovipositional phase was extended. Khattat and Stewart (1977) found that the preovipositional phase of *L. lineolaris* decreased as the temperature increased. Strong, et al. (1970) reported that the preovipositional phase of *L. hesperus* females held at 16 and 21°C was 17 and 12.3 days, respectively. These results support the temperature effect on this phase reported in this study.

Ovipositional Phase

The time period between the first and last oviposition is the ovipositional phase. The mean length of the ovipositional phase of *A. tristis* for each temperature is given in Table II. This phase ranged from 14.2 to 114.8 days and was significantly different ($P<0.05$) at each temperature. At 31.1°C the oviposition period unexpectedly increased to 79.3 days. This increase may be explained by hormonal secretions or that this temperature was the optimum oviposition temperature which would increase the egg laying period. The low temperature of 23.3°C appeared to increase the oviposition period by decreasing the daily oviposition per female. This is similar to the results of Beard (1940) and Nechols (1987) who reported that adults which emerge between late May and mid June have longer reproductive periods. High temperature has a major effect on female squash bugs as the total number of eggs and egg masses increased from 23.3 to 31.1°C. Beard (1940) reported that during the summer, the greatest number of eggs were laid on the hottest day. The results of this study showed that the shortest oviposition period occurred at 35.6°C. This could be explained by the exhausting effect of temperature on the female.

Senescent Phase

The senescent phase is the period from last oviposition by the female until her death. This phase averaged 6.6, 5.5, 3.7, and 5.2 days at 23.3, 26.7, 31.1, and 35.6°C, respectively. No significant differences in the mean length of the senescent phase were found (Table II). Female squash bugs spend similar amounts of time postovipositionally with no apparent temperature effect.

Proportional Reproductive Parameters

Since significant differences occurred in the times spent in three of the four phases discussed above. The proportion of time spent by each female in each phase was calculated by dividing the time spent in each stage by the total longevity. No significant differences were found in this set of data (Table III). This is evidence that the differences in time spent were due to temperature and not to changes in bionomics. Overall proportional times were averaged for each phase across temperatures (Table III). This information will be useful in simulation experiments.

TABLE III

MEAN PROPORTIONAL LENGTHS OF REPRODUCTIVE LIFE CYCLE PHASES OF A. TRISTIS AS AFFECTED BY TEMPERATURE

Temp (^oC)	n	Prem. Mean	s.d.	Preov. Mean	s.d.	Ovip. Mean	s.d.	Senes. Mean	s.d.
15.6	6	--	--	--	--	--	--	--	--
23.3	5	.07a	0.01	.06a	0.06	.82a	0.07	.04a	0.04
26.7	6	.09a	0.03	.03a	0.02	.78a	0.13	.09a	0.09
31.1	6	.07a	0.02	.02a	0.01	.86a	0.05	.04a	0.03
35.6	5	.09a	0.01	.08a	0.06	.60a	0.31	.22a	0.31
Overall	22	.08	0.02	.05	0.04	.77	0.18	.10	0.16

Means within a column followed by the same letter are not significantly different (P>0.5; Duncan's multiple range test)

Fecundity

Fecundity of adult female A. tristis is defined as the total number of eggs laid by a female during her lifetime. At 15.6°C the insects were largely immobile, did not mate, and no oviposition occurred. It is believed that 15.6°C represents the developmental threshold of A. tristis (Fargo and Bonjour, 1987). These authors found that eclosion did not occur at this temperature although the eggs were still viable. Beard (1940) and Nechols (1987) reported that cold weather reduced squash bug activity and increased the proportion of insects entering diapause.

Fecundity increased with temperature from 23.3 to 31.1°C. Total oviposition per female averaged 489.8, 352.5, 744.7, and 182.2 eggs at 23.3, 26.7, 31.1, and 35.6°C, respectively. No significant difference in mean eggs per female existed between 23.3 and 26.7°C (Table IV). Fecundities at these temperatures were significantly different ($P<0.05$) from those found at the two higher temperatures. Egg production was greatest at 31.1°C and lowest at 35.6°C. Previous researchers reported that A. tristis laid an average of 150 (Girault, 1904), 356 (Wadley, 1920), and 409 (Beard, 1940) eggs per female.

The largest mean number of eggs per mass (15.9) occurred at 23.3°C. The maximum was 55, produced by an individual female at 31.1°C. Beard (1940) found that the number of eggs deposited in each mass was highly variable with a maximum of 47.

Mean eggs per mass in this study averaged 15.9, 10.9, 13.6, and 11.7 at 23.3, 26.7, 31.1, and 35.6°C, respectively (Table IV). Wadley (1920), Beard (1935 and 1940), Elliot (1935), and Bonjour and Fargo (unpublished) reported average eggs per mass of 15.4, 14.2, 16.9, 15.0 and 19.5 eggs, respectively, which were similar to the findings in the present research.

TABLE IV

EFFECT OF FIVE CONSTANT TEMPERATURES ON THE FECUNDITY OF A. TRISTIS FEMALES

Temp. °C	n	Total Egg Masses	Total Eggs	Mean Mass /Female	s.d.	Mean Eggs /Female	s.d.	Mean Eggs /Mass
15.6	6	--	--	--	--	--	--	--
23.3	5	154	2449	30.8a	4.82	489.8a	58.08	15.9
26.7	6	194	2115	32.3a	4.40	352.5a	52.99	10.9
31.1	6	329	4468	54.86	4.40	744.7b	52.99	13.6
35.6	5	78	911	15.6c	4.82	182.2c	58.05	11.7

Means within a column followed by the same letter are not significantly different (P>0.05; LSD).

Daily fecundity rates for each temperature were calculated by dividing the total eggs per female by the corresponding longevity period. The results show that the daily average fecundities per female were 3.5, 5.2, 8.1, and 7.5 at 23.3, 26.7, 31.1, and 35.6°C, respectively. Means at 23.3 and 26.7°C were not significantly different ($P>0.05$) but were significantly lower than those at 31.1 and 35.6°C (Table V). The highest fecundity rate was at 31.1°C and the lowest was at 23.3°C.

More egg masses per female per day were laid at 35.6°C and significantly fewer egg masses were laid at 23.3°C than at the other temperatures (Table V). Previous studies from the field and laboratory reported that larger egg masses and higher egg numbers were laid per day than those observed in our study. Beard (1940) reported that the number of eggs deposited in each mass was variable and egg laying occurred during higher temperatures averaging ten eggs per day.

Table VI shows that the squash bug reached maximal egg production during the first week of oviposition under the two upper temperatures of 31.1 and 35.6°C. The data showed that the cumulative daily percentage of eggs laid was more concentrated during the first two weeks. At the two lower temperatures, 23.3, and 26.7°C, maximum egg-laying was reached during the 3rd and 2nd week of oviposition, respectively. These data agree with Beard (1940) who found that under field conditions, 70% of the eggs were deposited during the first 3 weeks under cool weather.

TABLE V

EFFECT OF FIVE CONSTANT TEMPERATURES ON DAILY FECUNDITY (TOTAL FECUNDITY/MEAN LONGEVITY) OF A. TRISTIS

Temp (°C)	n	Eggs Per Female	s.d.	Egg Masses Per Female	s.d.
15.6	--	--	--	--	--
23.3	701	3.5a	0.4	.22a	0.03
26.7	405	5.2a	0.5	.48b	0.04
31.1	554	8.1b	0.4	.59bc	0.04
35.6	121	7.5b	0.9	.65c	0.08

Means within a column followed by the same letter are not significantly different (P>0.05; LSD)

TABLE VI

EFFECT OF CONSTANT TEMPERATURES ON MAXIMAL WEEKLY EGG PRODUCTION OF *A. TRISTIS*

Temp (°C)	Eggs/Week	Week
23.3	99	3
26.7	111	2
31.1	153	1
35.6	148	1

Egg Viability

No eggs were deposited at 15.6°C. This would indicate that 15.6°C is below the reproductive threshold of A. tristis. Beard (1940) reported that 15.6°C or above is required for reproductive activity. He also reported that reproductive failure may occur because low temperatures prohibit the development of sexual organs.

Percent viability averaged 88.4, 93.4, 79.7, and 66.3% at 23.3, 26.7, 31.1, and 35.6°C, respectively. Viabilities at 23.3 and 26.7°C were not significantly different (Table VII). They were, however, significantly higher than those at 31.1 and 35.6°C.

The highest viability occurred at 26.7°C and the lowest at 35.6°C. Elliot (1935) and Beard (1940) found that viability of A. tristis eggs averaged around 96% at 23.3°C. At 35.6°C, more than 50% of the nymphs died shortly after hatching. Fargo and Bonjour (1987) found similar results in that egg eclosion did not occur at temperatures above 33.3°C. Champlain and Sholdt (1967) reported that 40°C was lethal to eggs of G. punctipes. An inverse relationship exists between 23.3 and 35.0°C but dropped considerably above 35.0°C. Clair and McPherson (1980) and Strong and Sheldahl (1970) reported that viability in E. tristigmus and L. hesperus was also inversely related to temperature and that only 6% of the eggs laid at 35°C hatched. Khattat and Stewart (1977) found that the percent of eggs which hatched of L. lineolaris also decreased with increasing temperature.

Comparison of viability through the first three weeks of oviposition of A. tristis females showed that viability at 35.6°C was significantly lower ($P<0.05$) than those at 23.3, 26.7, and 31.1°C during each of the first three weeks (Table VIII). High egg viability at 23.3 and 26.7°C agrees with Elliot (1935) where viability of A. tristis ranged from 94.6-96.7% during July in Connecticut. Egg

TABLE VII

TEMPERATURE EFFECTS ON A. TRISTIS EGG VIABILITY

Temp °C	Total Eggs	Total Hatch	n	% Viab.	s.d.	No. Viab. Eggs[a] Per Female/Day
15.6	--	--	--	--	--	--
23.3	2449	2171	78	88.4a	1.9	3.1
26.7	2115	1978	46	93.4a	2.5	4.9
31.1	4468	3297	70	79.7b	2.0	6.4
35.6	911	683	13	66.3c	4.7	5.0

Means within a column followed by the same letter are not significantly different at the 5%level.
[a]% viability/day = no. eggs per female/day * viability.
Comparisons were made between total egg numbers.

TABLE VIII

TEMPERATURE EFFECTS ON EGG VIABILITY (% TOTAL EGGS LAID) FOR THE FIRST THREE WEEKS OF OVIPOSITION OF A. TRISTIS

Temp °C	n	Week 1	s.d.	n	% Viability Week 2	s.d.	n	Week3	s.d.
15.6	-	--	--	-	--	--	-	--	--
23.3	5	92.2a	3.2	5	94.5a	3.3	4	90.0a	7.2
26.7	6	95.8a	3.0	6	93.1a	3.0	5	94.3a	6.6
31.1	6	95.8a	3.0	6	95.9a	3.0	6	91.1a	6.6
35.6	5	75.8b	3.2	4	73.6b	3.3	4	47.1b	7.2

Means within a column followed by the same letter are not significantly different (P>0.05; Duncan's multiple range test).
Comparisons were made between total egg number.

hatch at 23.3, 26.7, and 31.1°C showed similar values over the first three weeks and were not significantly different from each other. These results show that during the first three weeks, viability at 23.3, 26.7, and 31.1°C maintained a consistent pattern. The sharp decline in egg viability at 35.6°C indicates that this temperature approaches the lethal temperature for eggs.

Viability at 23.3 and 26.7°C was consistent during the 20 weeks of oviposition. At 31.1°C viability was generally lower during weeks 6-13, and particularly during weeks 11-13. Viability at 35.6°C showed a similar pattern to that at 31.1°C but was limited to 3 weeks. Viability decreased rapidly during the last weeks of oviposition at 31.1 and 35.6°C. This might be explained by high temperatures exhausting the females and reducing oviposition and egg viability. Another possibility is that high temperatures cause females to oviposit large numbers of viable eggs during the first weeks after which they become exhausted and inactive.

Egg Development

Table IX illustrates the mean egg development times for A. tristis at different constant temperatures. Developmental time generally decreased with increasing temperatures. Development was significantly longer ($P<0.05$) at 23.3°C and shortest at 31.1 and 35.6°C. Development time was intermediate at 26.7°C and was significantly different from the other temperatures. These development times are similar to those reported by Fargo and Bonjour (1987) who found times of 12.6, 8.5, and 6.6 days at 23.3, 26.7, and 31.1°C, respectively. Butler and Wardecker (1971) and Isenhour and Yeargan (1980) also found that the duration of egg development decreased significantly ($P<0.05$) with each increase in temperature for Lygus hesperus and Orius

TABLE IX

MEAN DURATION (DAYS) OF A. TRISTIS EGG STAGE AT DIFFERENT CONSTANT TEMPERATURES

Temp. (°C)	Duration	Range	S.E.
15.6	--	--	--
23.3	11.5a	11-14	0.6
26.7	9.6b	8-13	0.7
31.1	6.6c	5-8	0.5
35.6	6.6c	6-8	0.5

Means within a column followed by the same letter are not significantly different at the 5% level (Duncan's multiple range test).

insidiosus. Beard (1940) reported that at 23.3°C and relative humidity of 62%, 11 days were required for egg development.

CHAPTER V

SUMMARY AND CONCLUSION

Reproductive bionomics of adult squash bugs were studied at five constant temperatures: 15.6, 23.3, 26.7, 31.1, and 35.6°C. Data included information on longevity, reproductive life cycle, fecundity, egg viability, and egg development (data summarized in Table X). Very definite temperature effects were found in all aspects of A. *tristis* reproductive bionomics.

Overall means for longevity were 179.6, 166.5, 88.4, 132.6, and 29.6 days at 15.6, 23.3, 26.7, 31.1, and 35.6°C, respectively. Male longevity ranged from 36.0 to 193.6 days and that for the female was 23.3 to 171.3 days in this range of temperatures.

The reproductive cycle of the female squash bug was found to be characterized by four phases: premating, preoviposition, oviposition, and senescence. The average premating time at these temperatures ranged between 2.0 and 9.4 days. A range of 2.0 to 8.6 days was required after mating to oviposition. The ovipositional phase ranged from 14.2-114.8 days, and senescence varied from 3.7 to 6.6 days in the temperature regimes examined.

Fecundity under four constant temperature regimes was also investigated. The total number of egg masses produced ranged from 78-194. Total eggs per female varied between 182.2 and 744.7 eggs. Daily fecundity per female varied between 3.5 and 8.1 while average daily egg masses produced per female ranged from 0.22-0.65. Viability ranged from 66.3% to 93.4%. Egg development time ranged between 6.6 and 11.5 days.

TABLE X

SUMMARY OF THE EFFECT OF TEMPERATURE ON THE REPRODUCTIVE BIONOMICS OF THE SQUASH BUG, A. TRISTIS

Temperature	Longevity		Reproductive Cycle				Fecundity		%	Egg Develop
°C	Male	Female	Prem	Preov	Ovp	Senes	Tot Eggs	Tot Eggs/Female	Viability	Days
15.6	187.8	171.3	--	--	--	--	--	--	--	--
23.3	193.6	139.4	9.4	8.6	114.8	6.6	2449	489.8	88.4	11.5
26.7	110.3	66.5	5.3	2.2	53.5	5.5	2115	352.5	93.4	9.6
31.1	173.8	91.3	6.2	2.2	79.3	3.7	4468	744.7	79.7	6.6
35.6	3.6	23.2	2.0	2.0	11.2	5.2	911	182.2	66.3	6.6

The information collected in this study indicates that temperature has a major effect on the bionomics of Anasa tristis. Adult squash bugs were able to survive at the low temperature (15.6°C) but they were inactive during this period and did not mate or oviposit. Adults under the higher temperature (35.6°C) were active and produced a tremendous number of eggs during the short time they lived.

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