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I am submitting herewith a thesis written by Anita M. Baker entitled "Fecundity, Fertility, and Longevity of Podisus maculiventris (Say): With Notes on Mobility Impairment." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science, with a major in Entomology.

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FECUNDITY, FERTILITY, AND LONGEVITY OF *PODISUS MACULIVENTRIS* (SAY): WITH NOTES ON MOBILITY IMPAIRMENT

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

Regularly expressed fecundity occurred in always paired Podisus maculiventris females, and in those which had been paired for 48h, 96h, 144h, 192h. Virgin females did not display regularly expressed feundity laying larger egg batches less frequently. Egg cluster size frequencies and modes were not significantly different among females which had copulated. There were no significant differences among the mean cumulative, or daily fecundity rates, for any females, indicating that fecundity was not affected by the amount of time they were paired with males. There was no peak or subsequent daily decline in fertility corresponding to the duration of the experimental period. Mean fertility of never paired females differed significantly from those paired. The mating system of females in this study was described as convenience polygamy.

The average life spans of always paired and virgin females were significantly different, however, increasing paired time from 48h - 192h did not contribute to reduced longevity. Longevity of mobility impaired females was not significantly different from that of non-impaired females.

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INTRODUCTION

Podisus maculiventris (Say), the spined soldier bug, is an indigenous predator commonly collected throughout North America east of the Rocky Mountains. The species is predaceous on a number of crop and forest insect pests (McPherson 1980). Its effectiveness as a predator has been demonstrated against the Mexican bean beetle, the soybean and cabbage loopers, the variegated cutworm, and several lepidopterous pests of apple (Waddill and Shepard 1974, Ignoffo et al. 1977, Marston et al. 1978, Ables and McCommas 1982, Mukerji and LeRoux 1965).

The apparent value of P. maculiventris as a potential biocontrol agent stimulated evaluation of various aspects of its life history and bionomics (Kirkland 1897, Morrill 1906, Esselbaugh 1948, Mukerji and LeRoux 1965). A procedure was established by Mukerji and LeRoux (1965) to rear laboratory colonies of P. maculiventris. Prior to that time investigations were limited to field studies and small-scale studies of individual laboratory specimens. Growth and development processes of the spined soldier bug have been determined (Landis 1937, Esselbaugh 1946, Mukerji and LeRoux 1965, 1969b, 1969c, Warren and Wallis 1971). The predatory nature of P. maculiventris has been studied in both the field and laboratory (Morris 1963, Mukerji and LeRoux 1969a, Coppel and Jones 1962, Waddill and Shepard 1975).

Insects which prey upon and parasitize P. maculiventris have been reviewed (Coppel and Jones 1964, Yeargan 1979). The relationships between fecundity, fertility, longevity, and mating of lab-reared P. maculiventris, have not been fully investigated.

Fecundity and fertility have been considered specific elements of the reproductive capacity of insects (Harris and Todd 1980a). It has been determined that the reproductive capacity of beneficial predators is important to their success in both field and laboratory applications. Though reproductive capacity is largely genetically predetermined for the species, it is dependent in some respects on mating and copulation (Chapman 1982).

Longevity of beneficial predators is also important to their success in field and laboratory applications (Waddill and Shepard 1974, Ignoffo et al. 1977). Like reproductive capacity, the limits are predetermined for the species and modified by the environment. The imposition of unusual environmental stimuli may induce significant changes in longevity.

The objectives of this study were to investigate relationships between fecundity, fertilty, and mating of P. maculiventris females; to investigate statistically the possibility of reduced longevity as a function of increased paired time in P. maculiventris females; to

determine the effect of mobility impairment on longevity of P. maculiventris females, since previous testing (Ignoffo et al. 1977) was done only over a short period of time; and to assess the practical implications of this information.

CHAPTER I

LITERATURE REVIEW

The spined soldier bug was known from 1851 until 1899 as Podisus spinosus Dallas. In 1899 Scudder reprinted an overlooked paper by Thomas Say (1831) which contained the original description. The description named the spined soldier bug Pentatoma maculiventris, a specific name which preceeded Dallas' spinosus by 20 years (Blatchley 1926). In a generic revision, Schouteden (1907) synonymized Podisus with Apateticus. Van Duzee (1909) disclaimed the synonymy and divided the group into two distinct genera, Podisus and Apateticus. The species is currently recognized as Podisus maculiventris (Say) (Blatchley 1926).

Field and laboratory evaluations were conducted on feeding and reproductive behavior, life stages, nymphal appearances, and seasonal activity of P. maculiventris (Kirkland 1897, Morrill 1906, Whitmarsh 1916). Esselbaugh (1948) provided additional details, resolved discrepancies, and summarized life history data. Life history and habits of laboratory-reared P. maculiventris were later determined (Mukerji and LeRoux 1965, Warren and Wallis 1971).

Eggs were described by Olsen (1910) and Esselbaugh (1946) and detailed information on the external

morphology of the spined soldier bug egg was recently provided by Hinton (1981) and Lambdin and Lu (1984). Nymphal development rates, mortality rates, and stadia duration were determined using a variety of prey (Landis 1937). Duration, behavior, and qualities of the life stages of lab-reared P. maculiventris were characterized using two different rearing methods (Mukerji and LeRoux 1965, Warren and Wallis 1971). Quantitative studies on food consumption and growth, and energetics supplemented the data (Mukerji and LeRoux 1969b, 1969c).

The predaceous habits of the spined soldier bug have been studied and numerous prey species have been referenced (Landis 1937, Mukerji and LeRoux 1965, McPherson 1980). The most recent host list included 111 prey species in 41 families representing eight orders (McPherson 1980). Predatory behavior has been documented on several important pests (Waddill and Shepard 1975, Ignoffo et al. 1977, Marston et al. 1978, Ables and McCommas 1982). The process of ingestion, including feeding and ingestion rates was described with Galleria mellonella L. and Tenebrio molitor L. as prey species.

The predaceous behavior of P. maculiventris has been further described according to various components of functional response. Prey defense, and age of the adult predator, had very important effects on the functional response of the spined soldier bug. Both factors encour-

aged selective predation of smaller, younger prey. Increased adult predator age resulted in levelling off of cumulative predation (Morris 1963). Mukerji and LeRoux (1969a) found similar response behavior but included in their study the functional responses of nymphs. They found that increased nymphal age resulted in an increased ability to subdue prey and a faster consumption rate. High prey densities were determined to accelerate predation while low prey densities allowed survival but resulted in the production of abnormally small spined soldier bugs (Hokyo etal. 1975).

Fecundity, Fertlity, and Mating

Some general aspects of the reproductive capacity of lab-reared Podisus maculiventris have been determined. Couturier (1938) suggested that oviposition continued until death of the female provided she was kept with a male. Mukerji and LeRoux (1965) found that females became sexually mature within 24 hours after adult emergence, could mate as many as 7 - 10 times during a life span, and were polygamous. In addition, they estimated the mean number of eggs/cluster to be between 18 and 31, and the mean number of egg clusters laid over a lifetime to be between 13 and 16. Mukerji and LeRoux (1965) predicted that the number of fertile eggs laid depended upon the number of matings and the length of life. Warren and Wallis (1971) supported those findings

and suggested that removal of a male from a cage which contained a fertile female would result in decreased, and finally cessation of fertility.

In their study on the southern green stink bug, Nezara virulda (L.), Harris and Todd (1980a) defined fecundity and fertility as specific elements of the reproductive capacity of insects. The effects of mating on fecundity and fertility under laboratory conditions have been investigated for several stink bugs (Mithcell and Mau, 1969; Youther and McPherson, 1975; Nilakhe, 1976; Harris and Todd, 1980a).

The relevance of multiple copulation is unclear. Chapman (1982) suggested that for many insects a single copulatory act provided the female with sufficient sperm to fertilize most of the eggs she produced. A possible selective advantage to the increased diversity of offspring resulting from copulation with different mates has been acknowledged (Thornhill and Alcock 1983). Copulation appeared to stimulate both oogenesis and oviposition in some species (Chapman 1982). A comprehensive study of insect mating systems indicated that in many insects, including some pentatomids, a polygamous nature resulted from convenience not requirement (Thornhill and Alcock 1983). Youther and McPherson (1975) found that for Euschistus servus (Say), the brown stink bug, multiple copulations had no effect on fecundity or

fertility over an eight week period. They also reported that the fecundity of once-mated, twice-mated, thrice-mated, and mated-for-life females was not significantly different. No significant differences were found between fecundity of once-mated and always-mated female rice stink bugs, Oebalus pugnax (F.) (Nilakhe 1976). The females laid fertile eggs long after the death of their mates.

The fecundity of virgin stink bug females has also been evaluated. Significant differences were found between fecundity of mated females and unmated females for the southern green stink bug and the brown stink bug (Mitchell and Mau 1969, and Youther and McPherson 1975 respectively). The fecundity of virgin rice stink bug females was not significantly different from those which were mated (Nilakhe 1976).

Longevity and Mating

Pearl (1928) postulated an inverse relationship between the "rate of living" and the length of life. This relationship has been acknowledged for P. maculiventris and other insects according to their reproductive capacity. Couturier (1938) indicated increased ovarian activity as a cause of reduced longevity in laboratory-reared P. maculiventris females. He attributed the increased activity to stimuli from the male. Other investigators have noted the discovery of

prematurely dead females bloated with eggs (Esselbaugh, 1948; Mukerji and LeRoux, 1965).

Unmated females of several species have longer lifespans than their mated counterparts. Examples include: cockroaches (Periplaneta americana (L.)), milkweed bugs (Oncopeltus fasciatus (Dallas)), southern green stink bugs (Nezara virulda), dermestid beetles (Trogoderma versicolor Creutz), and brown stink bugs (Euschistus servus), (Griffiths and Tauber 1942, Lener 1967, Mitchell and Mau 1969, Davis 1945, and Youther and McPherson 1975). For N. virulda, the difference could be as exaggerated as 50% (Mitchell and Mau 1969).

Mobility Impairment

Mass release of beneficial insects for insect pest control is an established practice (Huffaker 1971, DeBach 1974). Efficacy of predators is often reduced by their natural tendency to disperse (Ignoffo et al., 1977). Beneficial insects are difficult to recapture as soon as 24 hours after their release (Waddill and Shepard, 1974). The idea of mobility impairment, especially by dewinging, was suggested by Ignoffo et al. (1977) to increase retention of beneficials and to enhance the possibility of additional predation by the progeny of the impaired individuals. In that study, impaired and non-impaired P. maculiventris females were released into test plots and counts were made after 72 hours. More impaired

females were recaptured and significantly greater numbers of eggs were found in test plots with impaired females.

CHAPTER II

METHODS AND MATERIALS

General Rearing Conditions

Laboratory rearing of *P. maculiventris* required constant food and water sources, suitable rearing containers and regulated environmental conditions including temperature, humidity, and photophase. Experiments were conducted from 5 January, 1983, through 20 December, 1983, in an environmentally controlled room in an insectary at the University of Tennessee's Plant and Soil Sciences Farm. Experimental conditions were modified from rearing methods of Mukerji and LeRoux (1965), Warren and Wallis (1971), and Evans (1982a).

Colonies of the greater wax moth, *Galleria mellonella* (L.), were maintained to provide a constant source of live food. Wax moth larvae were reared in plastic containers on a commercially prepared diet produced by Bio-Serve Inc. (1983). One sixth or seventh instar waxworm was provided daily to each spined soldier bug.

P. maculiventris specimens were reared in 100 X 15 mm Fisher Brand plastic petri dishes. The dishes were stacked approximately 42 mm beneath an artificial light fixture containing one 130 cm Sylvania 40W Gro Lux and one 130 cm Sylvania 40W Cool White florescent light bar. Each dish set-up contained a filter paper lining

(9.0 cm coarse texture disc) and a 12 X 35 mm shell vial for water. The vial was filled with distilled water and a cotton plug approximately 10 mm long. The water supply was replenished as necessary. The order in which the petri dishes were stacked was alternated daily throughout the experiment. The room containing all spined soldier bugs was maintained at 80-86°F, 40-50% RH, and 8D:16L photophase.

Fecundity, Fertility, and Mating

Treatment groups consisted of two-day-old adult P. maculiventris females as follows: treatment 1, 10 females always paired with males; treatment 2, five females never paired; treatments 3,4,5,6, five females each, paired with males for 48h, 96h, 144h, 192h respectively. The term "paired" refers to confinement together of female and male, not to copulation. The sample size was doubled in treatment 1, (compared to other treatments), to compensate for expected reductions in non-zero observations since always paired females faced a greater threat of male cannibalism. Computerized calculations resolved any differences in sample number so that statistics were relative to the sample size.

Eggs were removed daily by transferring the surface they were laid on (top, bottom, or lining of petri dish, or water vial) to a new dish set-up. The dish set-up of

the female was then restored. Eggs were observed daily during a five day incubation period beneath the lights.

The experiment conformed to randomized complete block design. Tests were run for 35 days with each test replicated three times for a total of 3675 observations. Data were collected daily for number of eggs laid and number of eggs hatched. In this study, the term fecundity refers to expressed fecundity, or the actual number of eggs laid rather than oocyte production (a definition confirmation by Labeyrie, 1978). Fertility refers to the actual reproductive capacity as measured by the production of viable offspring. Observations of eggs laid and eggs hatched for females which died during the experiment were recorded as zero.

Longevity and Mating

Treatments and number of observations were the same for this section as those for the fecundity, fertility, and mating section. Longevity was determined by recording the number of days lived by each insect in each treatment group.

Mobility Impairment

Treatment groups consisted of 16-day-old adult P. maculiventris females as follows: treatment 1, 15 dewinged females; treatment 2, 15 females marked with acryllic paint; treatment 3, 15 females both marked and

dewinged; treatment 4, 15 non-impaired females. Virgin, singly reared females were examined to exclude the possibilities of male cannibalism or increased ovarian activity from the longevity comparisons.

The dewinging procedure involved clipping of the wings with irridectomy scissors at the axillary region. The marking procedure, which facilitates ease of location for recapture, caused only limited immobility (probably due to a weight factor). All insects were maintained in the lab until death. Longevity was determined for each insect in each treatment group by adding the number of days lived after impairment to the initial age.

Analysis of Data

All statistical values were computer generated using SAS82. Cluster size frequencies and modes were calculated from the number of eggs laid using a frequency procedure which tabulated the number of times each cluster size occurred. Means and ranges were calculated for each variable (number of eggs laid, number of eggs hatched, number of days lived, number of days lived post impairment). Analysis of variance was done with a general linear models procedure which calculated an F-value for each variable, and the probability associated with the F-value. Least significant ranges were calculated for each of the variables using Duncan's new multiple range test for mean separation. Regression analysis was con-

ducted on fecundity and fertility data with percent hatch the dependent variable, and cluster size the predictor.

CHAPTER III

RESULTS AND DISCUSSION

Fecundity, Fertility, and Mating

Cluster size frequency. Data from this study indicated that regularly expressed fecundity would occur in females which had been paired for only 48h, 96h, 144h, or 192h. Expressed fecundity of those females was similar to that of always paired females. Cluster size frequency and cluster size mode for each of those groups was indiccative of the similarities (table 1, figures 1-5). Other studies indicated cluster size modes, or typical number of eggs/cluster for always paired females, ranging from 14 to 30 (Mukerji and LeRoux 1965, Warren and Wallis 1971, Lambdin, unpublished). The data from this study, for females paired 48h, 96h, 144h, 192h, and always paired females, fit that range.

A cluster size mode for females never paired could not be readily established (table 1, figure 6). A cluster size mode for virgin P. maculiventris females was not reported in previous studies. Cluster size frequency for never paired Euschistus servus females was determined and a cluster size mode was established; however, the data was significantly different from that of females which had been paired.

Copulation probably stimulated females to begin ovipositing which resulted in expressed fecundity. Females in all of the paired groups copulated at least once and displayed regularly expressed fecundity, whereas the never paired females had no opportunity to copulate and did not display regularly expressed fecundity. Their egg clusters contained greater numbers of eggs laid less frequently. This may have resulted from a lack of copulatory stimuli. Once oviposition began, there did not appear to be further requirements for copulatory stimuli.

Table 1. Egg Cluster Modes, Ranges, and Totals for Podisus maculiventris (Say) Females

TRT	EGGS/CLUSTER		CLUSTERS/35 DAYS
PAIRED	MODE	RANGE	NO.
always	14,15	1-52	15.4
never	--	1-41	10.0
48h	21	1-47	17.8
96h	14	1-47	16.6
144h	15,17	2-65	18.1
192h	14	1-57	14.9

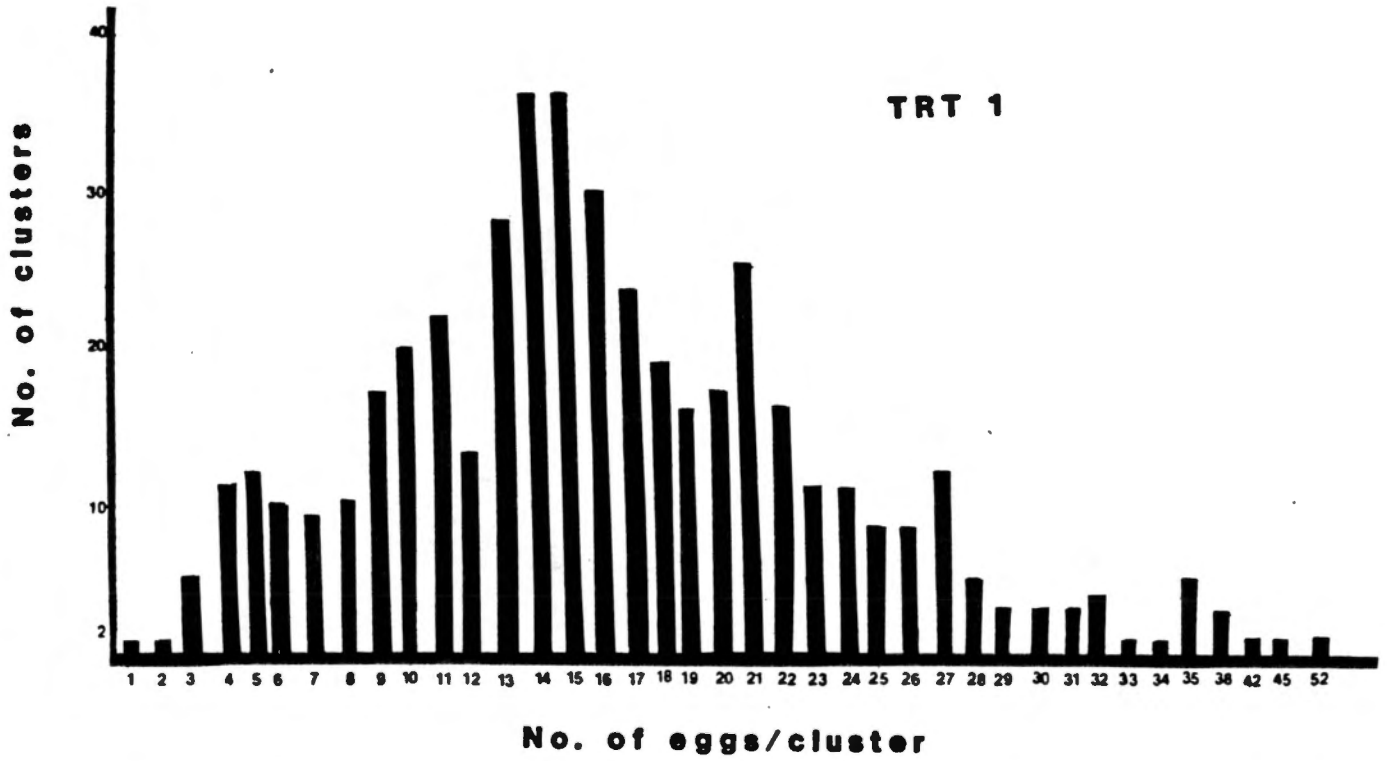


Figure 1. Cluster size frequency for Podisus maculiventris (Say) females always paired

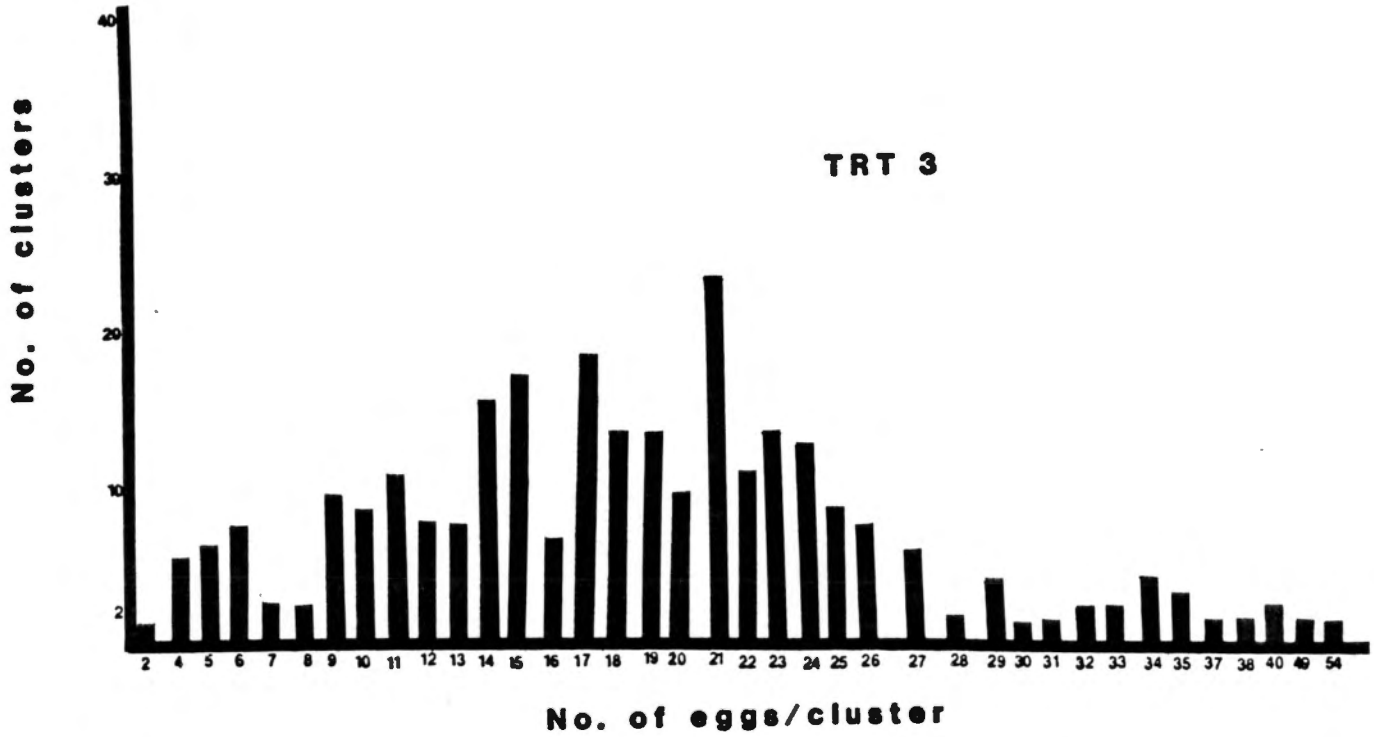


Figure 2. Cluster size frequency for Podisus maculiventris (Say) females paired 48 hours

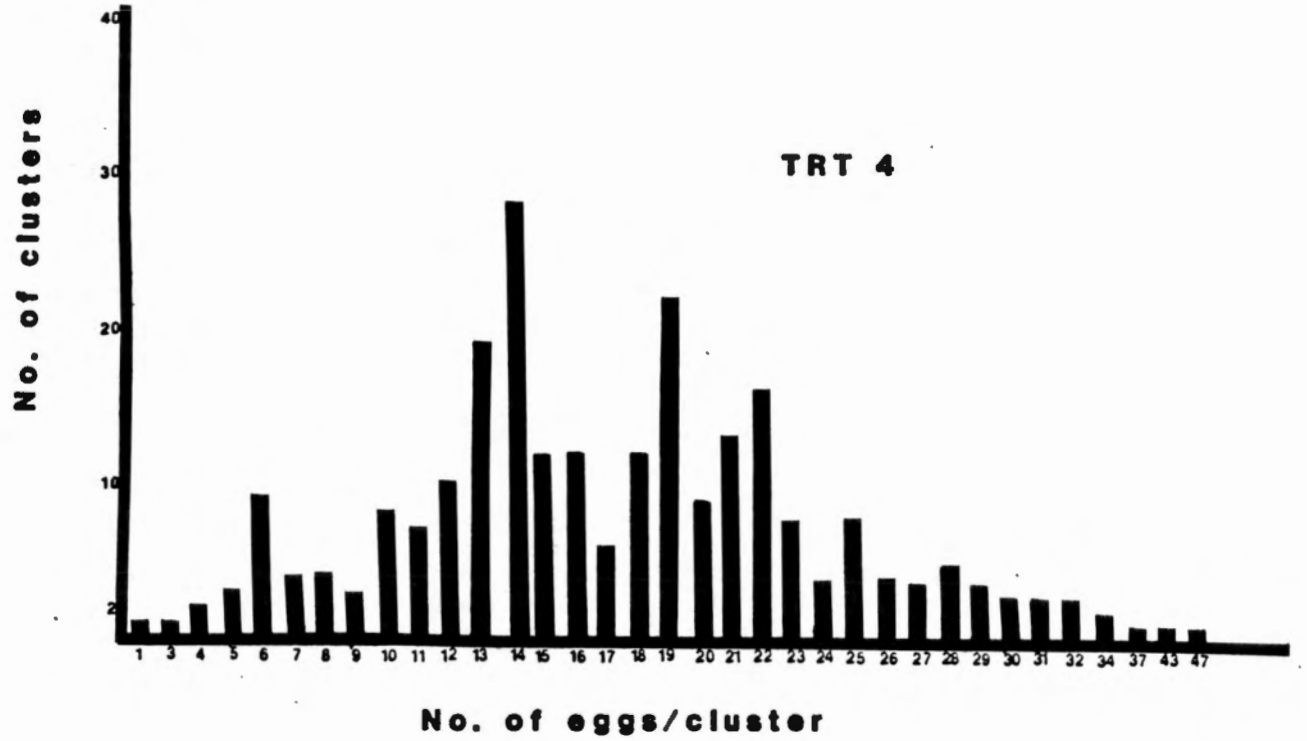


Figure 3. Cluster size frequency for Podisus maculiventris (Say) females paired 96 hours

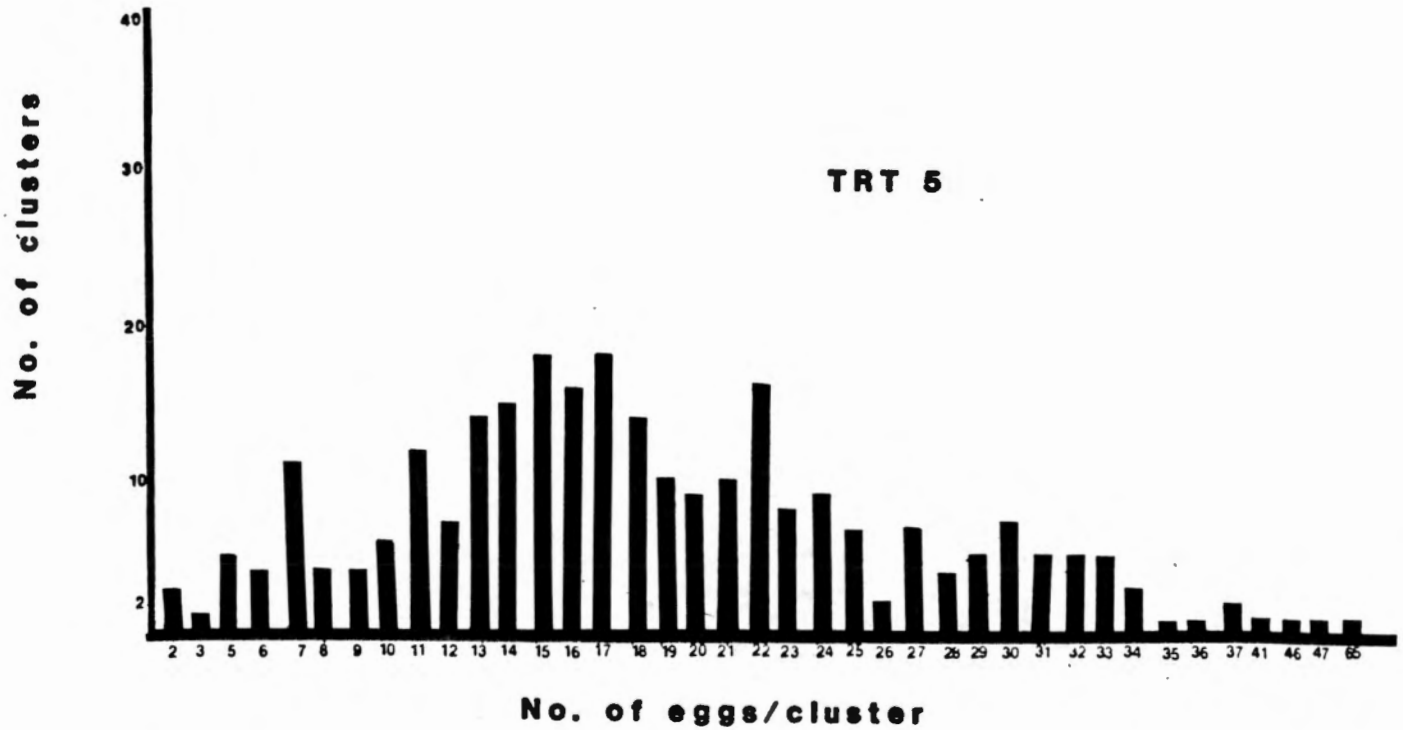


Figure 4. Cluster size frequency for Podisus maculiventris (Say) females paired 144 hours

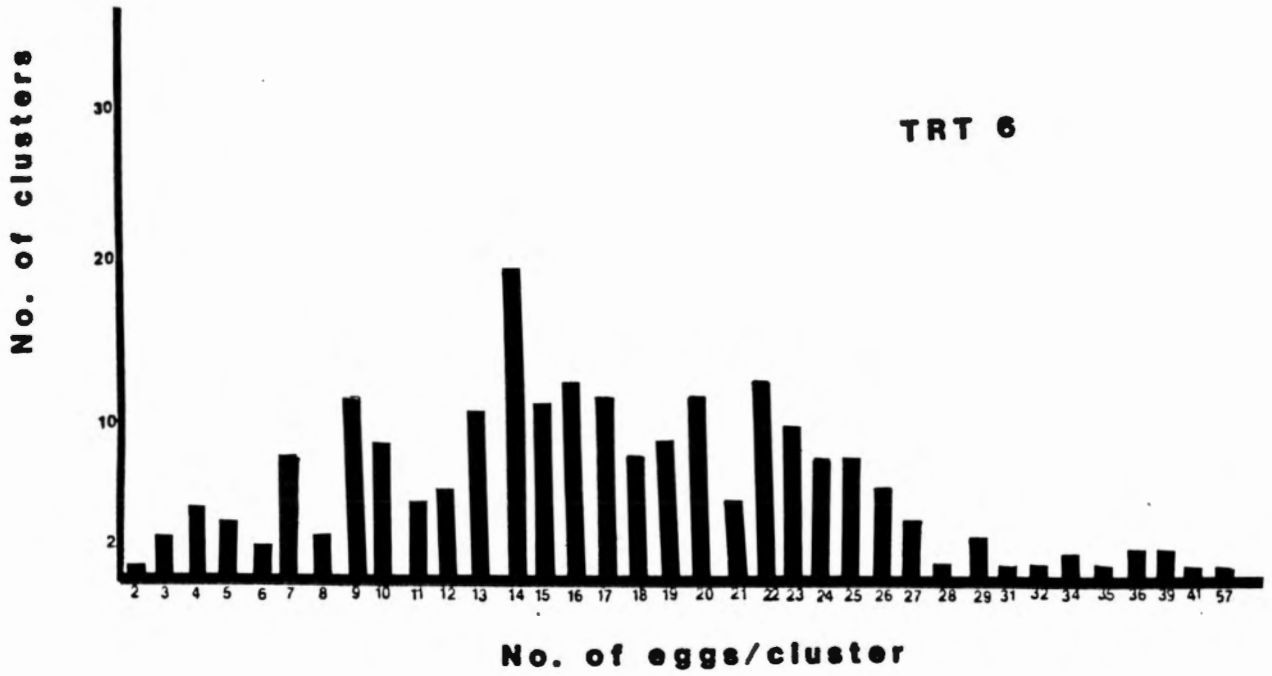


Figure 5. Cluster size frequency for Podisus maculiventris (Say) females paired 192 hours

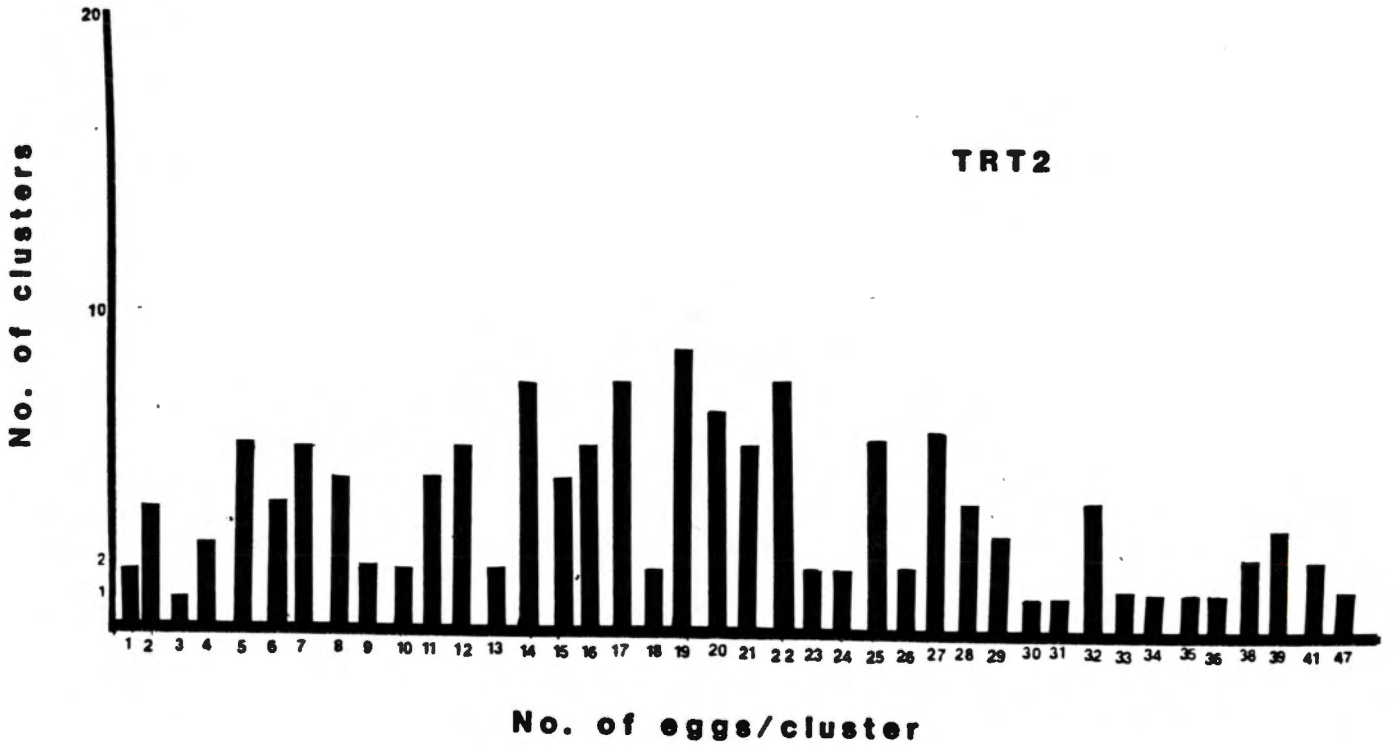


Figure 6. Cluster size frequency for Podisus maculiventris (Say) females never paired

Cluster size data exposed a general trend in the relationship between fecundity and fertility of lab-reared P. maculiventris females which had copulated (females always paired, and females paired 48h, 96h, 144h, and 192h). Larger egg clusters contained greater numbers of infertile eggs. This tendency was especially pronounced during the beginning (day 1-3) of the test period. The inverse relationship between cluster size and percent hatch was not nearly as pronounced throughout the duration of the experimental period. Fertility records for the final period (day 30-35) were distorted as several females had died and therefore were not producing viable offspring. When the data for dead females was excluded, the inverse relationship between hatch and cluster size also appeared diminished in the final period. Regression analysis of the predictability of percent hatch from cluster size produced a negative parameter estimate which was indicative of the inverse relationship between cluster size and fertility. The estimate was non-significant and resulted at least in part from the diminishing of the inverse relationship. Virgin females were excluded from this trend since they never laid fertile eggs.

Other possible factors which influenced the relationship between cluster size and cumulative fertility of females which had copulated, included infertility and

periodic productivity. Infertile females produced egg batches throughout the experiment, but never produced viable offspring. There were infertile females in all groups which had been paired with males (table 2). Those factors contributing to infertility were not evaulated. A major possibility was unsuccessful sperm transfer which can result from incapability of either male or female.

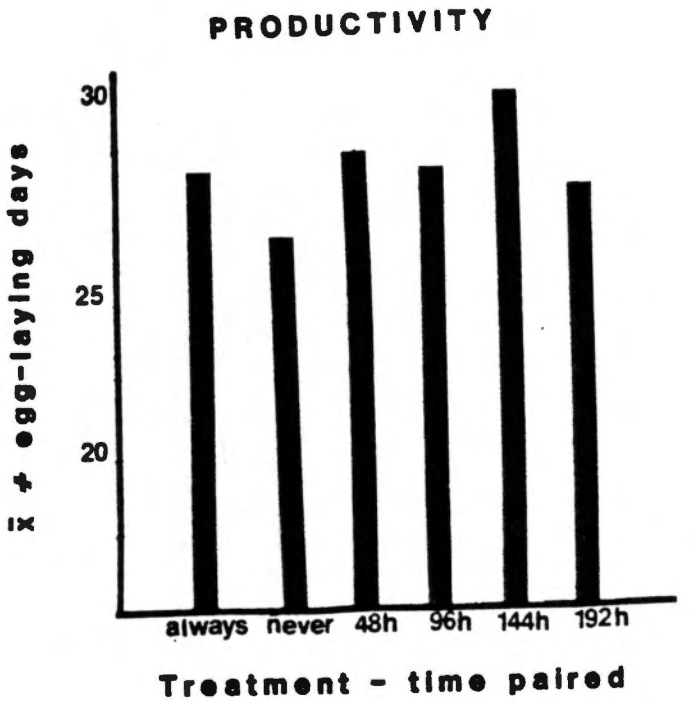
Table 2. Number of Infertile Podisus maculiventris (Say) Females per Treatment Group for 35 Days

TRT PAIRED	N	NO. of INFERTILE FEMALES	% INFERTILITY
always	30	5	16
never	15	15	100
48h	15	3	20
96h	15	3	20
144h	15	4	26
192h	15	5	33

The length of paired time probably didn't influence infertility since all of the females had sufficient time to copulate and were observed doing so. Though variation among individual fertility rates was high, error calculations did not suggest significant experimental error.

Infertile females in this test were probably the result of random occurrence which should be accounted for if mass rearing is being considered. From these observations, infertility of about 20% of females throughout the test could be expected, as well as possible infertile periods at the begining of the test, and reduced offspring production due to female death toward the end of a 35 day period.

All females had periods of productivity interspersed with nonproductivity during the 35 day test. Average productivity periods for all females ranged from 1-16 days during which egg clusters were laid. Average non-productivity periods generally lasted only 1-2 days after which oviposition resumed (except for never paired females where it could become quite extended). Virgin females had fewer productive days than any paired females (figure 7). Always paired females, and those paired 96h and 192h respectively, had productivity rates slightly lower than the females paired 48h and 144h. The rates corresponded with the slightly reduced longevity for those females. All observations for females which died during the experiment were recorded as zero.



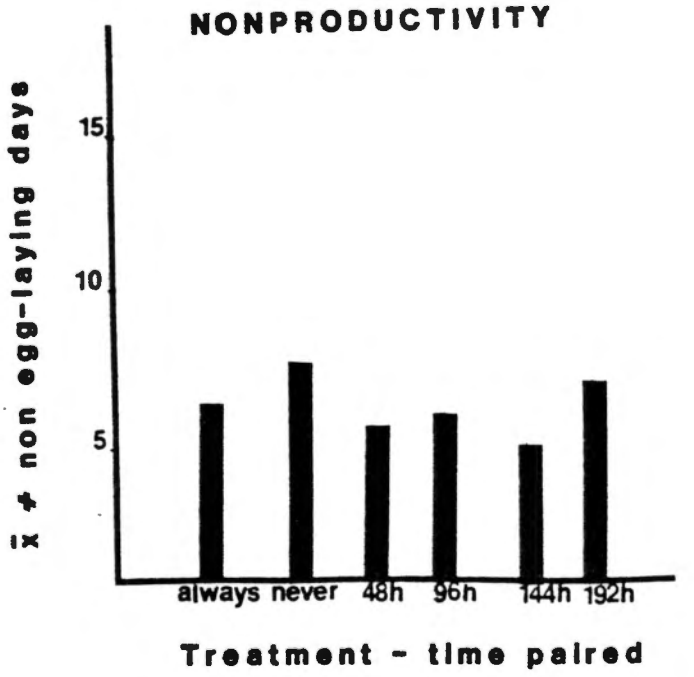


Figure 7. Mean productivity and nonproductivity periods of Podisus maculiventris (Say) females

Average fecundity and fertility rates. Mean fecundity and fertility rates for the paired females in this study differed somewhat from fecundity and fertility rates reported in other studies (table 3). Mukerji and LeRoux (1965) observed higher fecundity and fertility rates, as well as longer life spans for P. maculiventris females. Their insects were maintained in the lab at 70°F which was determined, in the same study, to double the average life span compared to insects reared at 80°F. (The average life span of the insects in the Mukerji and LeRoux study was nearly 4X longer than the insects in this study; however, the total fecundity of the insects was only about 25% greater.) The longer life spans of the females apparently allowed for higher fecundity rates. Warren and Wallis (1971) reported fecundity rates very similar to the data obtained in this study. No previous data was available for comparison of fecundity rates of virgin females. Previously recorded rates for mean daily fecundity (Mukerji and LeRoux 1965, Warren and Wallis 1971) were not significantly different from those produced in this study (table 4).

Fertility rates recorded by Mukerji and LeRoux (1965) represented the percent hatch of 10 select batches of eggs ranging from 78% - 100%. The cumulative fertility rates in this study represented a percentage of eggs hatched from all eggs laid over a 35 day period per

treatment group (table 3). Fertility rates for insects within treatment groups ranged between 78% - 100% on select days, but the overall fertility rates for 35 days were lower (around 50%). Daily fertility rates for the data in this study were calculated (table 4), but none were available for comparison from other studies.

Table 3. Mean Cumulative Fecundity and Fertility Rates, and Fecundity and Fertility Ranges for Podisus maculiventris (Say) Females

TRT PAIRED	FECUNDITY MEAN	FECUNDITY RANGE	FERTILITY MEAN	FERTILITY RANGE	PERCENT HATCH
always	270.2 a	38-526	135.2 a	0-395	50
never	197.3 a	14-464	-- b	--	0
48h	334.5 a	147-483	140.3 a	0-401	42
96h	292.9 a	66-504	162.7 a	0-469	56
144h	367.0 a	79-577	136.6 a	0-475	37
192h	257.4 a	31-196	102.8 a	0-409	40

Table 4. Mean Daily Fecundity and Fertility Rates and Ranges for Podisus maculiventris Females

PAIRED	AVG. LAID/DAY	RANGE	AVG. HATCHED/DAY	RANGE
always	7.7 a	1-15	3.8 a	0-11
never	5.3 a	1-13	0.0 b	---
48h	9.6 a	1-14	4.0 a	0-13
96h	9.6 a	1-14	4.6 a	0-13
144h	9.8 a	1-16	4.0 a	0-14
192h	7.3 a	1-14	3.0 a	0-12

Note: Any two means followed by the same letter are not significantly different ($P<0.05$ Duncan's New Multiple Range Test).

Analysis of variance--fecundity. Analysis of variance for fecundity indicated no significant differences among means of the six treatment groups, for daily fecundity rates or overall fecundity, at the 5% level of significance. The fecundity of P. maculiventris females in this study was not affected by the amount of time they were paired with males.

No other data for fecundity of P. maculiventris females with restricted paired time was available for comparison. However, expressed fecundity for paired P. maculiventris females can be compared to that of its phytophagous relatives, the southern green, brown, and rice stink bugs. Fecundity rates of brown stink bug females with restricted mating exposures were not found to be significantly different from females which had always been mated (Youther and McPherson, 1975). Fecundity of always mated female rice stinkbugs, Oebalus pugnax, and of those which were exposed long enough for only a single copulation was not significantly different (Nilakhe, 1976).

Virgin spined soldier bug females in this study were equally as fecund as their mated counterparts. They laid fewer egg clusters, less frequently, but the clusters tended to be larger than those of paired females. Their cumulative fecundity was less than that of any other group but not small enough to be significantly different.

This was also observed for the rice stink bug (Nilakhe, 1976). The fecundity of virgin brown and southern green stink bugs was significantly different from those which were allowed to copulate (Youther and McPherson, 1975 and Mitchell and Mau, 1969).

Analysis of variance--fertility. Mean fertility of never paired females was significantly different from all other females at the 5% level of significance. No significant differences occurred among the mean fertility rates of the paired females (table 3). The fertility data obtained in this study reflected the ability of P. maculiventris females paired for restricted times to maintain their fertility relative to always paired females. Previous studies suggested that the presence of males was necessary for continued fertility in the lab, and that a decline in fertility would be evidenced if the male was removed from the female (Couturier 1938, Mukerji and LeRoux 1965, Warren and Wallis 1971). Though some females had marked periods of infertility near the end of the test, and some were infertile throughout, there was not a noticeable peak or subsequent daily decline in the fertility of the insects in this study corresponding to the duration of the experimental period.

Although no fertility data on P. maculiventris was available for comparison, fertility rates of other pentatomids have been examined. Youther and McPherson

(1975), found no significant differences in the fertility of females of E. servus with restricted mating exposure and those mated for life. Harris and Todd (1980a, 1980b) observed numerous copulations by the southern green stink bug, but similar fertility rates between always mated females and females isolated after one copulation.

The fact that P. maculiventris females can and will copulate more than once probably does not necessitate their doing so. Results from this study suggested their polygamous nature was one of convenience. P. maculiventris females seem to exemplify insects which display polygamous behavior even though limited exposure to one male can provide sufficient sperm for continued fertility (Thornhill and Alcock 1983). This was not uncommon for other pentatomids (Harris and Todd 1980b), or for species in other hemipteran families. Polygamous behavior appears to result from lack of a preventative mechanism. It may also allow for additional input of sperm if an original fertilization attempt fails. Added benefits may be the contribution of additional oviposi-tional stimuli. Convenience polygamy does not require repeated copulation. It does not necessarily add to genetic diversity of the progeny either, as any success-ful sperm transfer probably serves to fertilize all eggs that the female produces (Thornhill and Alcock, 1983).

Longevity and Mating

Mean longevity. Previous longevity records for paired P. maculiventris females were quite variable, but encompass the records generated in this study (table 5). Mukerji and LeRoux (1965) recorded longevity for lab reared, paired females ranging from 115 to 191 days at 70°F. Warren and Wallis (1971) recorded mean longevity for paired females as 84.7 days at 70°F. Mukerji and LeRoux also recorded mean longevity for lab reared, paired females as 61.3 days at 80°F. Field collected females had much shorter average life spans, ranging from 1 - 26 days, at 80°F (Mukerji and LeRoux 1965).

Table 5. Mean Longevity of Podisus maculiventris (Say) Females

PAIRED	N	MEAN NO. DAYS LIVED
always	30	25.7 c
never	15	35.0 a
48h	15	31.9 ab
96h	15	28.3 bc
144h	15	33.5 ab
192h	15	28.1 bc

Note: Any two means followed by the same letter are not significantly different (P<0.05 Duncan's New Multiple Range Test).

Analysis of variance--longevity. Analysis of variance for mean longevity did not indicate significant differences among the means of the four groups which were paired for restricted periods. However, a significant difference between always paired and never paired females was indicated (table 5). Mean longevity of females paired for 48h and 144h was similar to that of the never paired females, whereas mean longevity of females paired for 96h and 192h was similar to that of the always paired females. There was no indication that increasing paired time contributed to reduced longevity. However, the slightly reduced longevity apparently affected fecundity and fertility rates (table 3, note always paired, 96h paired, 192h paired groups). Only the always paired and never paired conditions had distinct effects on longevity.

Significant difference in longevity between virgin and always paired females was not unexpected. Couturier (1938), and Mukerji and LeRoux (1965), noted a considerable difference between the life spans of virgin and mated P. maculiventris females; they did not express the difference in statistical terms. Three related insects (the milkweed bug, southern green stink bug, and brown stink bug) have demonstrated significantly different life spans as a result of their sexual activity.

Mobility Impairment

Longevity breakdown. Longevity data for mobility impaired females was broken down into periods for consideration of field application (table 6). The first period, 0-10 days, represented premature death since the average longevity of lab-reared virgin insects is between 60 and 80 days. Premature deaths in this case, were limited to the treatment groups and should be compensated for if field release is the goal. A small percentage of impaired females (especially dewinged) may die as a result of improper impairment. The second period, 11-30 days, represented a stage where insects might be used to help suppress pest populations in short season crops (eg. snapbeans). It is noteworthy that at least one-half of the spined soldier bugs remained alive throughout the period regardless of impairment. The third period, 31-50 days, represented a stage where the predator might be used to help suppress a pest population which had second or staggered generations. The final period, >51 days, included those individuals considered to be long-lived. Because the insects were 16 days old when the impairment occurred, they had lived upwards of 70 days. All 60 of the insects died within 76 days after impairment.

Table 6. Longevity Breakdown for Mobility Impaired, Virgin Podisus maculiventris (Say) Females

	NUMBER DEAD			
TREATMENT	0-10 DAYS	11-30 DAYS	31-50 DAYS	>51 DAYS
DEWINGED	3	4	4	4
MARKED	1	6	5	3
MARKED/ DEWINGED	1	7	2	5
CONTROL	0	7	3	5

Note: The table represents the number of females dying during each period.

Longevity comparisons. The actual number of days the insects lived varied (note ranges in table 7). Calculation of the mean and median for each group suggested that overall lifespans of the groups were very similar.

Table 7. Longevity Comparisons for Mobility Impaired, Virgin *Podisus maculiventris* Females

TREATMENT	MEAN	RANGE	MEDIAN
CONTROL	35.6 days	1-70 days	34.5 days
DEWINGED	30.8 days	1-67 days	33.5 days
MARKED	34.3 days	1-72 days	36.0 days
MARKED/ DEWINGED	37.5 days	1-76 days	38.0 days

Analysis of variance. No significant differences were indicated among the mean longevities of the four treatment groups at the 5% level of significance. This suggested that imposed conditions of mobility impairment did not significantly reduce longevity. Ignoffo et al. (1977) did not indicate reduced longevity as a result of mobility impairment for any of the experimental insects (*P. maculiventris*, *Campoletis flavicincta* (Ashmead), and *Hippodamia convergens* Guerin-Meneville) although their tests were conducted over a shorter period. The long term effect of impairment was important as the insects were no longer functioning under normal conditions. The spined soldier bugs in this test were hearty predators which withstood impairment without the duration of life being significantly reduced.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Cluster size frequencies and the cluster size modes of Podisus maculiventris females with limited paired time, and females always paired, were very similar. A cluster size mode for females never paired was not readily determined. Copulation probably provided a stimulus for the regularly expressed fecundity of the paired females, and the lack of it may have contributed to the lack of regularly expressed fecundity in the never paired females.

Cluster size data analysis indicated an inverse relationship between fecundity and fertility of P. maculiventris females which had copulated. Larger egg clusters contained greater numbers of infertile eggs. The relationship was especially pronounced during the begining of the test, and diminished thereafter.

Infertile females and periodic productivity affected the relationship between fecundity and fertility of P. maculiventris females in this study. About 20% of the paired females in this study were infertile throughout the experimental period. This result appeared to be a random occurrence and should be compensated for if mass rearing is attempted. P. maculiventris females had productive periods, during which eggs were laid, inter-

spersed with nonproductive periods, during which no eggs were laid. Virgin females had fewer productive days than any of the paired females. Productivity did not appear dependent upon copulation or presence of males.

Fecundity of the P. maculiventris females in this study was not affected by the amount of time they were paired with males. Virgin spined soldier bug females were as fecund as their mated counterparts though their cluster size frequencies and their productivity periods were somewhat different. Fertility of females paired for restricted times was not significantly different from the fertility of always paired females. Results from these tests indicated that for at least 35 days fertility could be maintained as the result of only limited exposure to a male in the lab. The results also suggested that the polygamous nature of P. maculiventris probably resulted from convenience and lack of a preventative mechanism, rather than requirement.

There were no significant differences in longevity of females paired for restricted periods and there was no indication that increasing the time spent paired with a male (up to 192h) would reduce longevity. The always paired and never paired conditions had distinct effects on longevity. Always paired females had significantly shorter life spans than their virgin counterparts.

Relationships between fecundity, fertility, longevity, and mating may have important practical implications. Results from these tests suggested no advantages in rearing continuously paired spined soldier bugs in the lab. Fecundity and fertility were not significantly increased as a result of constant exposure, and longevity was significantly reduced. Maintaining females without males (after copulation) requires less food. Maintaining insects at higher temperatures, though decreasing lifespans somewhat, allows for less energy input (spring, summer, temperate areas) without considerable reduction of progeny. The threat of cannibalism and increased ovarian activity are reduced by minimal paired time. The incidence of infertility, which appeared nearly constant for all pairing times, probably won't be increased as a result of restricted paired time. The fecundity and fertility rates, incidence of infertility, and average lifespans recorded in this study could be utilized to estimate potential production of offspring from a predator colony mass reared at 80°-86°F, with restricted paired time.

Mobility impairment did not cause reduced longevity in the lab. Further testing is necessary to determine its effects in the field. If those effects are negligible, as they are in the lab, then mobility impairment which limits or discontinues flight can be used to help

reduce dispersal. Predators restricted to walking, which is more time consuming, might leave more progeny to strengthen predation contributions to control situations.

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