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Reproductive Biology of *Lygus hesperus* Knight

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Esmat M. K. Hussein

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II. Biology of the Lygus Bug Sex Pheromone
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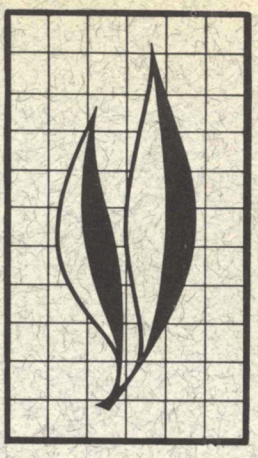

Studies on the reproduction biology of *Lygus hesperus* demonstrated that most adults first mated when they were 8 days old. The mating act lasted about 2½ minutes. Males could mate once per day for 6 consecutive days, but females only mated three times at 6-day intervals. One mating enables a female to oviposite viable eggs for the remainder of her life, which lasted an average of 38 days.

Virgin females began to produce a male-attracting sex pheromone as eggs matured within her ovaries; this first occurred when the adult female was about 6 days old. Pheromone release ceased immediately after mating, but was reinitiated 6 days later. In the fall, when the bugs entered diapause (characterized by atrophied ovaries) the pheromone was not released until diapause was terminated. During the period of diapause, males did not respond to the sex pheromone.

L. hesperus can be sterilized effectively by exposing the males to 5,000 rads of gamma radiation. Increased exposures affects the mating behavior by reducing male aggressiveness. The offspring from irradiated parents inherited a high degree of sterility; thus, a large proportion of the F_2 generation was sterile.

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Reproductive Biology of *Lygus hesperus* Knight[1]

INTRODUCTION

BUGS IN THE GENUS LYGUS are primarily pests of cotton, coffee, alfalfa, beans, carrots, and other crops grown for seed. The present control programs for these insects have been developed from detailed studies of their life history and behavior. When *L. hesperus* was first recognized as a pest of alfalfa seed 40 years ago, its life history in the Western United States was thoroughly described by Schull, *et al.*, 1934; Sorenson, 1939; Stitt, 1940; and King and Cook, 1932. Next damage studies were reported, records were published of numerous new hosts, and the destructive capabilities of *L. hesperus* and related species were described (Addicott and Romney, 1950; Baker, *et al.*, 1946; Davis, *et al.*, 1963; Carlson, 1964). Much research on *Lygus* spp. in the decade following World War II dealt with insecticidal control. In the last ten years, however, problems caused by chemical control have prompted studies on biology, ecology and physiology (Beards and Leigh, 1960; Leigh, 1963; Champlain and Butler, 1967), resistance to insecticides (Bacon, *et al.*, 1964), diapause (Beards and Strong, 1966), feeding behavior (Flemion, *et al.*, 1954; Landes and Strong, 1965; Strong and Landes, 1965), physiology of damage (Jeppson and MacLeod, 1946; Strong and Kruitwagen, 1968), nutrition (Auclair and Raulston, 1966; Strong and Kruitwagen, 1969; Vanderzant, 1967), parasitism (Clancy and Pierce, 1966; Clancy, 1968), flight activity (Stern and Mueller, 1968), new control methods with strip cutting (Stern, *et al.*, 1964) and host plant resistance (Lindquist, *et al.*, 1967).

No reports have appeared on the dynamics of lygus populations. The ultimate goal of any control program is to manipulate the population, not the individuals. Yet for most insects, including lygus bugs, the factors responsible for population performance are virtually unknown.

In reviewing the behavioral and physiological events leading to an increase of *L. hesperus* populations, we recognized a gross lack of understanding. For example, the simple act of mating, which in July occurs probably thousands of times daily in each acre of alfalfa, had only been observed three times by as many persons in the past 30 years. This act, essential for population maintenance and increase, had essentially escaped observation.

At Davis, *L. hesperus* has three generations per growing season. The relative numbers of insects per generation are shown in figure 1. These data have been compiled from several sources but stem mainly from sweep-net samples taken twice a week from portions of alfalfa hay fields left uncut for the entire 1968 season. When the remaining portions of the fields were harvested,

[1] Submitted for publication February 3, 1969.

the number of adults increased sharply the following day in the uncut portion. This increase is not reflected in figure 1 because it only lasted for a few days, and the plotted data in figure 1 are to represent the relative changes in numbers of *L. hesperus* in the absence of mass immigrations.

By mid-January all overwintering adults of *L. hesperus* are reproductive and the females begin egg laying. Although the data are incomplete, there is sufficient evidence to indicate that only the last group of eggs deposited by these females hatch, producing the spring nymphs labeled N1 in figure 1. This result is supported by Champlain and Butler (1967): their data indicate that the minimum developmental temperature for *L. hesperus* is 49°F, and that 225 day degrees (DD) are required for egg hatch. Eggs incubated at 49°F for 8–10 weeks failed to hatch which indicates that all eggs laid before February 10th would die, and those laid after this date would hatch around April 10–15, when 225 DD had accumulated. The spring nymph population gives rise to the first adult generation (A1), which in turn produces two additional complete generations. Nymphs hatching on or about August 20th are destined to become diapausing adults (Beards and Strong, 1966). Thus, about one-fourth of the individuals of the adult peak labeled A3 are nonreproductive and probably do not contribute to the overwintering adult population because they do not live long enough. The overwintering adults arise from nymphs produced by the reproductive members of A3. All surviving nymphs resulting from the A3 adults enter diapause upon reaching maturity. Diapause terminates during December after which the females become sexually mature, produce sex pheromones (see Part II), mate, and on warm days begin to lay eggs. Their eggs, upon hatching, give rise to the spring nymphs, completing the yearly cycle.

The time and temperature requirements for the complete development of *L. hesperus* (i.e., from egg to first egg) is about 945 DD (32 days at 80°F) but 1,380 DD are required for the completion of a generation. This discrepancy is caused by the change in rate of egg deposition as the females age (see the shape of the egg laying curve, figure 10). The mean age of all reproductive females in one generation was determined and compared to that of the next generation. When this was done, an indicated generation time of 45 days at 80°F, (or the equivalent of 1,380 DD) was obtained. As shown by the arrows on the day-degree curve in figure 1, increments of 1,350 DD correlate closely with the observed peaks of field-collected adults.

METHODS

Stock colonies of *L. hesperus* were maintained on fresh green beans (*Phasiolus vulgaris L.*) after the method of Beards and Strong (1966). Beans, grown locally during the summer or purchased from local groceries in the winter, were washed with detergent, rinsed, and patted dry before being used to replenish the bugs' supply. Fresh beans were placed in the cages twice weekly.

Oviposition cages were made from five-gallon cartons, each fitted with a screened lid, a window, and a sleeved entry port. Fresh beans were supplied twice weekly to provided food and oviposition sites. The entire stock colony was maintained at room temperatures (73°–80°F) and humidities (45–65 per cent RH) under 16 hours of light per day, supplied by cool white fluorescent lamps.

Bugs selected for the experiments were in the 5th instar stage; each bug

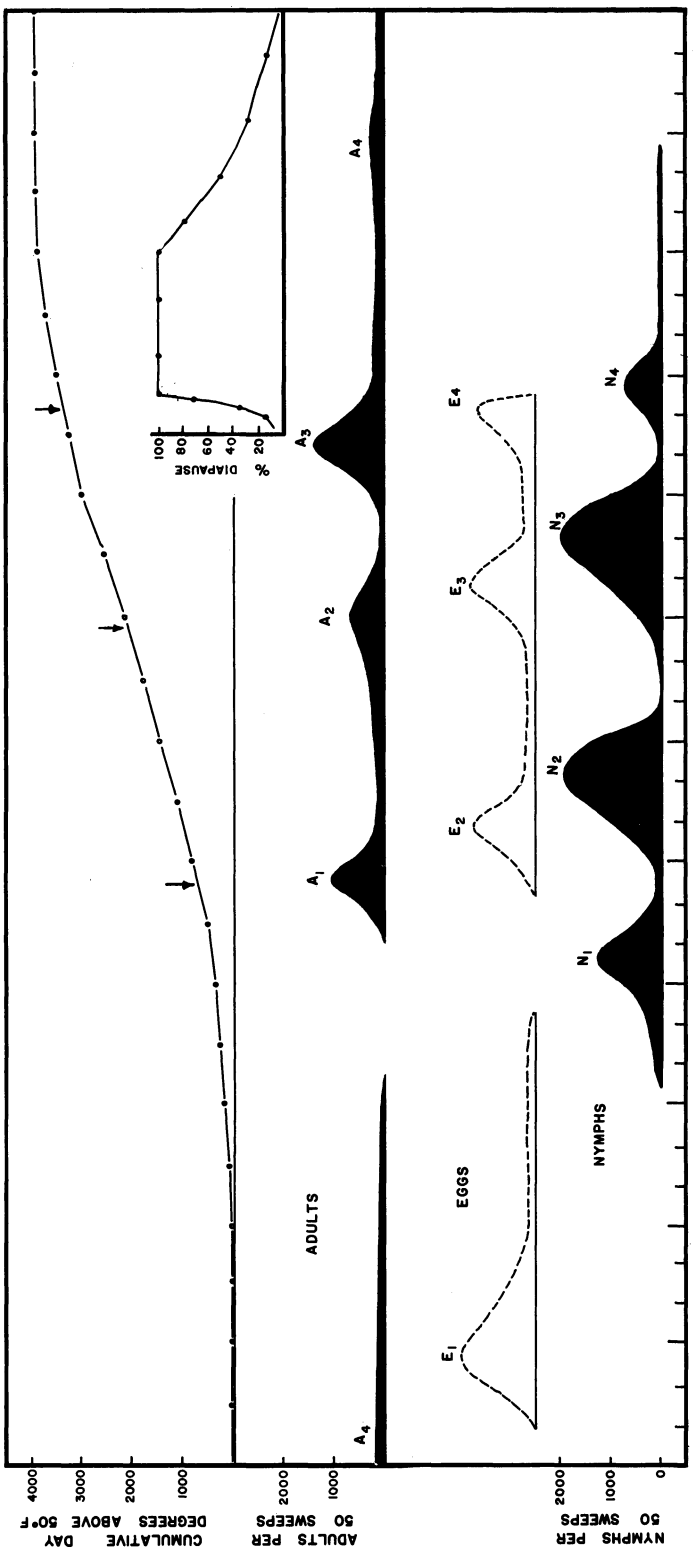


Fig. 1. Seasonal life history of *Lygus hesperus* at Davis, California. The egg curves indicated by dotted lines, are hypothetical. The curve for the cumulative day degrees above 50°F is based on normal Davis temperature records. The arrows indicate the number of day degrees for a complete generation as determined from laboratory studies.

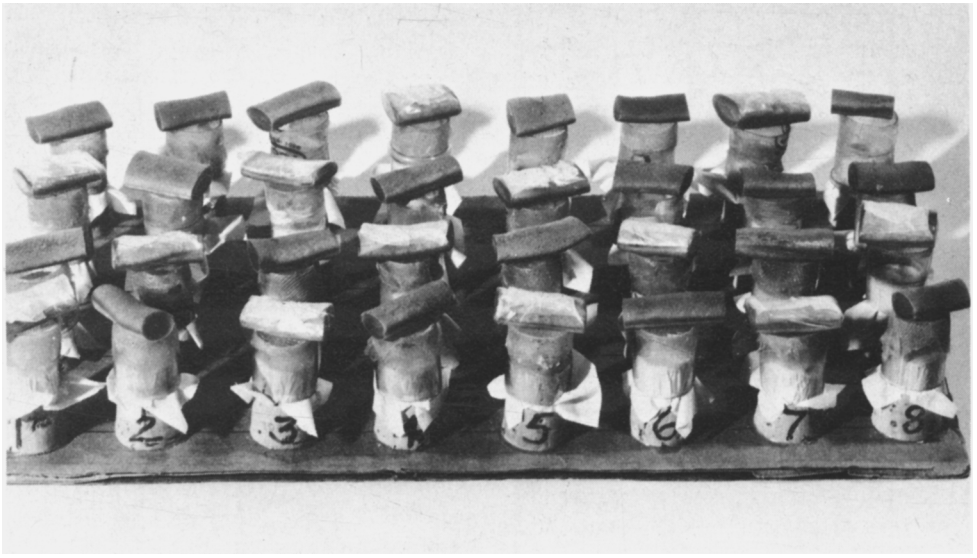


Fig. 2. Palletized individual rearing cages. One bug is placed in each cage. The bean sections are wrapped in parafilm when the females begin ovipositing, to prevent subsequent desiccation of the beans before the eggs hatched.

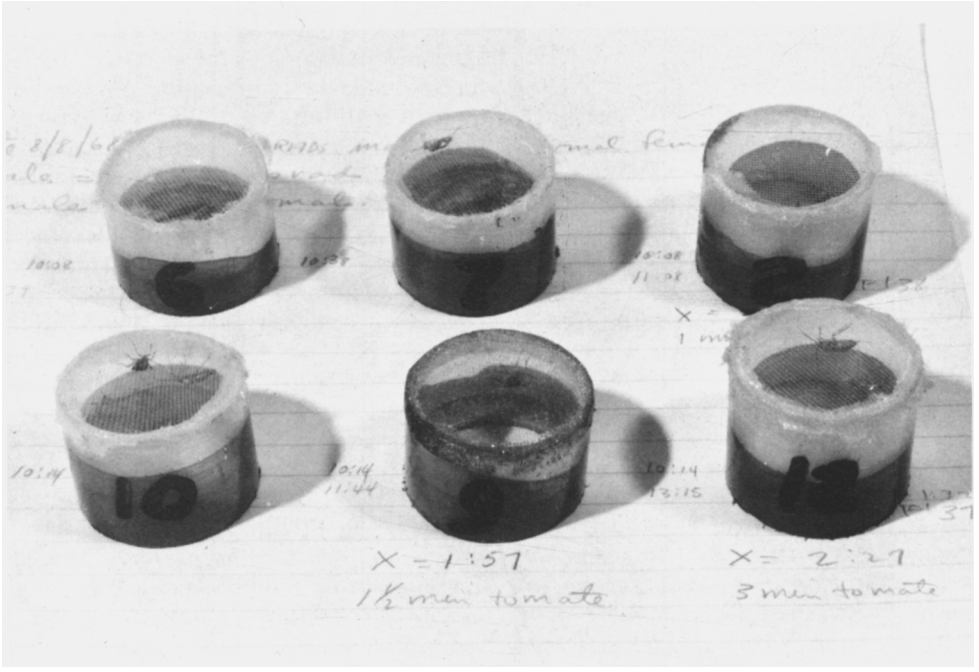


Fig. 3. Cages used for mating *Lygus hesperus*.

was placed in one of 32 individual cages glued on a 8-inch by 5-inch cardboard pallet. The cages were similar to those described by Landes and Strong (1965). Frequently several pallets were prepared simultaneously permitting detailed records on 200–300 bugs of similar age and sex. Pallets containing bugs were placed in an incubator at 80°F, 75 per cent RH, and 16 hours of light per 24 hours. Palletized bugs were fed fresh sections of green beans which were changed daily. These beans also served as oviposition sites permitting an accurate recording of the fecundity of the individual females. Figure 2 shows a pallet of individual rearing cages.

The mating cages were made from 1-inch sections of plastic test tubes (1-inch ID) whose inside surfaces had been abraded to provide a foothold for the bugs. The tops were covered with nylon hose while the bottoms were left open. Figure 3 illustrates several pairs of bugs in the mating cages.

For morphological studies etherized bugs were dissected under diluted Belar's (3:2) saline (Breland, 1961). Living sperm were observed with a phase-contrast microscope. Stained sperm were prepared with aceto-orcein following Breland's (1961) method. Histological preparations were made using the technique described by McManus and Mowry (1960). Tissues were embedded in Paraplast[R] and cut at 10 μ. Sections were stained with Harris's hematoxylin and counterstained with eosin.

I. LABORATORY STUDIES ON LYGUS REPRODUCTION[2]

Leigh (1963) and Champlain and Butler (1967) have adequately reported the general laboratory biology and life history of *L. hesperus*. Their studies, however, lack the details on reproduction *per se* that are crucial to studies on population dynamics. Therefore, this section presents information germane to the act of reproduction.

Mating behavior

When a male and a female of the appropriate age were caged together they were very active for 10–20 seconds, moving about haphazardly. Soon, however, they became quiet and remained motionless for a few seconds. Each partner then initiated a slow walk, and if the male touched the female with both antennae, an aggressive behavioral pattern immediately followed. This was characterized by a vertical jerking and quivering motion of his abdomen. If the male was on the female's right side he would move closer, bend his abdomen under the right side of the female's and attempt copulation. The male always directed the tip of his abdomen toward the right-hand side of the base of the female's ovipositor. If the female was receptive, copulation occurred. If not, she displayed an evasive behavior and eluded him. The male would then often repeat his aggressive courtship and occasionally the female would accept him.

Frequently, the male would mount the female and extend his abdomen but fail to do so from her right side. The female always rejected this pattern, as well as attempts to mount from the front or left side. If the male approached the female from the rear or her right side and she was receptive, they would simultaneously rotate toward each other until the tips of their abdomens touched. The male would then curl his abdomen under hers, enabling the genitalia to make contact at the base of the ovipositor.

[2] Taken in part from a thesis submitted in December, 1968, by J. A. Sheldahl to the Graduate Division, University of California, Davis, in partial fulfillment of the requirements of Master of Science degree.

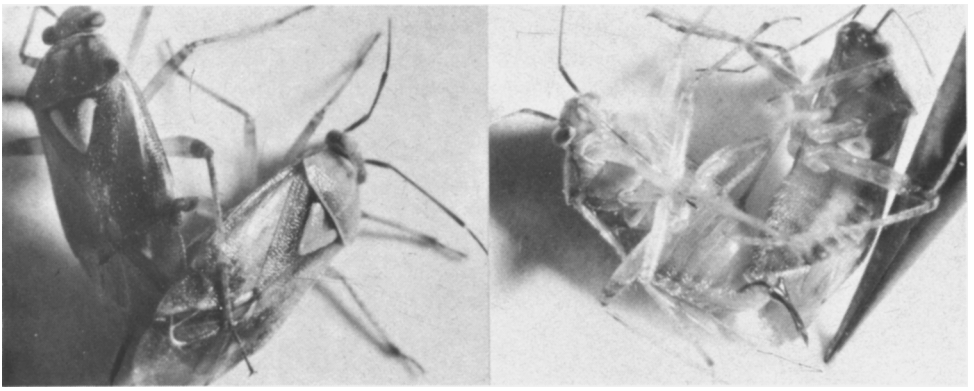


Fig. 4. Dorsal and ventral views of *Lygus hesperus* while mating.

While mating, the male always assumed the same posture: his left hind leg was over the female's hemelytra, and his body rotated about 45° to the right of hers. Just before the genitalia came in contact, the female flexed her ovipositor 180° so its tip extended posteriorly. Occasionally she would twist her body toward the male so they shared equally the imbalance inherent to the act.

On occasion, a female would display a receptive behavior even if the male was not aggressive. Generally, she would brace herself and slightly elevate her abdomen. If this behavior failed to elicit courtship by the male, the female would become aggressive by darting forward and tapping the tip of her abdomen against the substrate she was on. This action, which could be observed easily and heard readily from several feet, was usually followed by aggressive behavior of the male. Figure 4 illustrates the typical mating posture of *L. hesperus*.

Once in copula, the pair remained virtually motionless and seemingly oblivious to external stimuli for they could be picked up and handled without interrupting the act.

Interruption of copulation was always initiated by the male, who began to stroke the tip of the female's abdomen with his right hind leg. Shortly thereafter, the partners pushed away from each other and would suddenly snap apart. Occasionally the male would again attempt courtship but the female never accepted him, unless, for one reason or another, the pair happened to separate within a few seconds after initiating copulation.

While in copula, the ejaculatory organ could be seen through the male's seventh sternite. The pumping action started rapidly, but gradually slowed to about once in two seconds, whereupon copula would be terminated.

Duration of precopulation and copulation

Precopulation time was defined as the time from the moment the bugs were first introduced into the mating cage until copulation occurred. This interval, as well as the time in copula was measured. The data are summarized in table 1. The average precopulation time was 2 minutes and 42 seconds, whereas copulation lasted a mean of 2 minutes and 23 seconds. The precopulation time was used as a guideline during mating experiments. If mating had not begun after 6 minutes (about twice the average precopulation time) the attempted mating was usually terminated. Occasionally, a pair which had not begun mating by 6 minutes was set aside and left undisturbed, whereupon they copulated after 30–40 minutes. Six such ob-

TABLE 1

PRECOPULATION AND COPULATION DURATION OF *L. HESPERUS*

	Number of pairs	Mean duration	Range
		minutes	*minutes*
Precopulation	37	2:42	0:05 to 9:00
Copulation	163	2:23	1:10 to 4:55

servations were made but are not included in table 1 because such action did not appear to be within the realm of normal behavior.

Necessity of antennae

To determine the role of the antennae in mating, the terminal three segments (= flagellum) of the antennae were removed from 5th instar males and females. After maturing these individuals were given the opportunity to mate with normal individuals. (The excised appendages were absent in the newly molted adult.) All matings were attempted when the partners were 10 days old. Five of eight males having no flagella successfully mated with normal females (precopulation time was 3 minutes and 12 seconds). Three out of five females lacking flagella successfully mated with normal males, but the precopulation time averaged 16 minutes. When both partners had no flagella, only one of four pairs successfully mated, and this after 20 minutes. Thus, the flagellum was not considered a rigid prerequisite for normal mating, but because of the extended precopulation time, the antennae were somehow associated with mating.

Premating period

The premating period was defined as that time interval (in days) which elapsed between the imago molt and the youngest age when a virgin individual would mate. The premating period was determined by combining variously aged young and old individuals of opposite sex. The combinations were tested and the results are shown in table 2. The data indicate that, although both males and females were occasionally capable of mating when 3–4 days old, they most frequently mated when one of the partners was 6–8 days old and the other was at least that old. Young females (combined with old males) were generally not receptive until they were at least 5 days old. Young males, too, demonstrated little sexual aggressiveness for the first 4–5 days of adult life.

Frequency of multiple matings

Data concerning the frequency of mating are needed for the theoretical considerations of using sterile males for insect control.

Experiments to determine the frequency of mating were performed using 7–10 day old individuals reared on pallets. Six males were first mated to six females. On the following day, these same six males were given the opportunity to mate with six different virgin females, and on the third day with still six different virgin females. The reciprocal experiment using females and virgin males was simultaneously run. These tests indicated that males would mate on consecutive days and could frequently be induced to mate three to four times. Females, however, would never mate on consecutive days. In fact, 6–7 days was usually the minimum interval between female matings, although on occasion one would mate as early as 4–5 days after her initial mating. Females mated up to three times within 13 days and males up to five times in 5 days (and six times within a month). We did not

TABLE 2

PERCENTAGE OF SUCCESSFUL MATING WHEN MALES AND FEMALES OF *L. HESPERUS* WERE CAGED TOGETHER AT VARIOUS AGES*

Age of female in days	Age of male in days											
	2	3	4	5	6	7	8	10	15	17	20	29
1									0.0 (6)			
2									0.0 (13)			
3									0.0 (13)	25.0 (8)		0.0 (3)
4	0.0 (4)				0.0 (4)					0.0 (2)		0.0 (6)
5										50.0 (6)		
6										78.0 (9)		
7			75.0 (4)							75.0 (8)	50.0 (4)	
8							84.0 (44)					
9	0.0 (4)											
10					50.0 (4)				87.0 (15)			
18		0.0 (3)	0.0 (13)	50.0 (18)								
29		0.0 (3)	25.0 (8)									

* Top figure in each square indicates the percentage of successful matings; figure in parentheses indicates the number of pairs of bugs tested. Blanks indicate the combination was not tried.

TABLE 3

FREQUENCY OF MULTIPLE MATINGS BY *L. HESPERUS*

Frequency of mating	Number of adults			
	Males		Females	
	Attempts	Successes	Attempts	Successes
1 time	40	26	50	40
2 times	24	19	28	15
3 times	19	18	4	1
4 times	18	8		
5 times	8	2		
6 times	2	1		

TABLE 4

SUMMARY OF FECUNDITY DATA FOR 18 INDIVIDUAL *L. HESPERUS*

Female number	Time in copula	Total eggs laid	Hatch	Number of days of viable egg laying	Total number of egg laying days*	Viable-egg days/Total egg days
	minutes		*per cent*			*per cent*
1	1:55	388	21.1	13	33	.39
2	1:29	221	81.9	15	15	1.00
3	2:57	138	52.2	13	13	1.00
4	2:03	329	61.6	28	28	1.00
5	3:15	327	26.7	24	34	.71
6	3:28	259	25.9	24	33	.73
7	2:05	140	55.0	13	13	1.00
8	1:55	213	70.4	17	17	1.00
9	2:42	245	65.7	17	30	.57
10	1:50	274	58.4	17	17	1.00
11	2:06	345	13.6	13	33	.39
12	3:17	238	8.4	9	30	.30
13	2:05	237	55.7	19	19	1.00
14	2:53	393	90.3	26	26	1.00
15	—	201	12.9	7	23	.30
16	2:20	202	55.9	12	12	1.00
17	2:54	240	34.2	21	23	.91
18	1:40	243	6.9	8	24	.33

* Number of days after mating when females laid eggs, at least some of which hatched..

test females to see if they would mate more than three times. Every mating produced viable offspring, although accurate data on percentage of hatch were not recorded. The results of the multiple mating experiments are summarized in table 3.

Effectiveness of a single mating

The individual fecundity records of numerous females were examined and it was observed that egg hatch data were highly variable among females. In one group of 18 females, each individual was mated only once and was timed while in copula, and the percentage of her eggs that hatched was recorded daily. Regression and correlation analyses were computed between the mean percentage of hatch for each female during her entire life and 1) the length of time in copula and 2) the total number of eggs laid. Also, an attempt was made to correlate egg hatch with the age of the female when the eggs were laid.

These data, summarized in table 4, yielded no correlation between percentage of hatch and either the length of the mating period or the total number of eggs laid. Also, the percentage of hatch did not regress significantly with the age of the female. Nevertheless, as shown in the scatter diagram of figure 5, there was a significant change in percentage of hatch as the females matured. For the first 15 or so days after mating, about 50 per cent of the eggs hatched. From day 23 on, however, only about 12 per cent hatched, and this decreased to 0.0 per cent after day 30.

Correlation analyses were calculated in an attempt to explain some of the low egg hatches observed. For example, female number 12 (table 4) mated for 3 minutes and 17 seconds, laid more than the average number of eggs (238), but only 8.4 per cent of them hatched. Furthermore, she laid viable eggs for only 9 of her 30 egg laying days. By contrast 81.9 per cent of all eggs laid by female number 2 hatched, yet she mated only for 1 minute and 29 seconds.

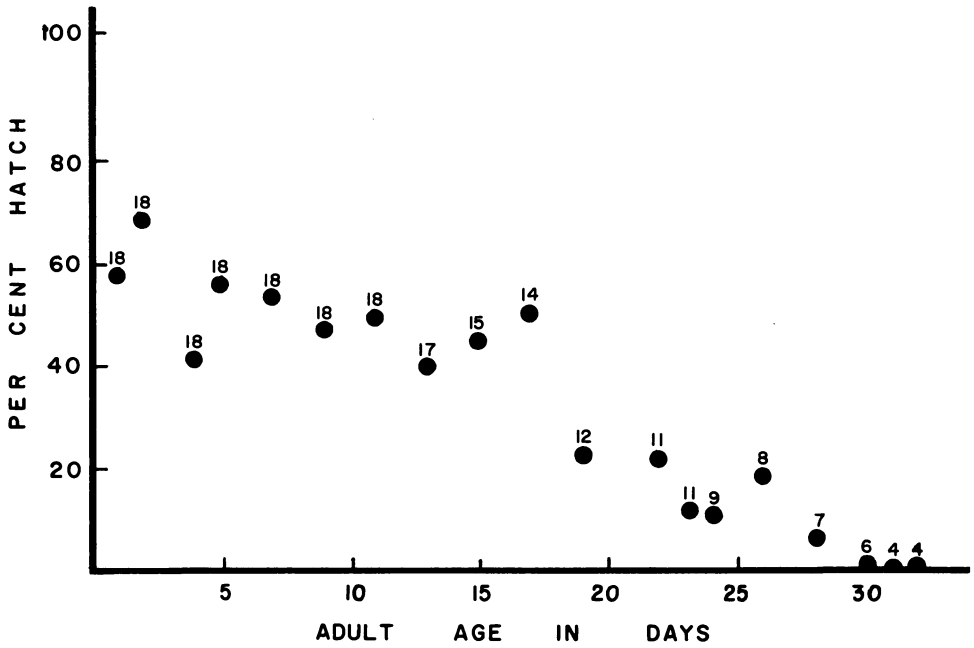


Fig. 5. Scatter diagram of *Lygus hesperus* mean egg hatch plotted against the age of the adult when the eggs were laid. The numbers above each point represent the number of females used in computing the point.

This variation can not be explained, but it appears to be a normal condition. It is suspected that the difference lies with the females and not their mates, for if the males were partially sterile, one would expect the percentage of hatch to be approximately the same when the same male mated with several females, as was done in the multiple mating experiments. This, however, was not the case; large differences in hatching were observed, even when the same father was involved.

The data in table 4 also illustrate that a single mating is sufficient for a female to produce viable eggs for her egg-laying life. Thus, the need for multiple matings is suspect.

Observations on the development of the reproductive systems of *L. hesperus*

As previously mentioned, neither males nor females normally mated until they were about 5 days old. To see if this phenomenon was correlated with maturation of the reproductive systems, both sexes were dissected daily and the development of the reproductive systems was recorded.

Males. The sexually mature male has a pair of large testes each composed of five testicular tubules. The seminal vesicle stores the sperm before ejaculation. Two pairs of semen-producing accessory glands are present. (See figure 6.)

The 5th instar males possess fully developed testes: squash preparations demonstrated that all stages of spermatogenesis were complete. Fully developed sperm and numerous sperm packets at the entrance of the seminiferous tubules were present. However, the 5th instar lacked completely the accessory glands and seminal vesicles. Thus the 5th instar has fully developed

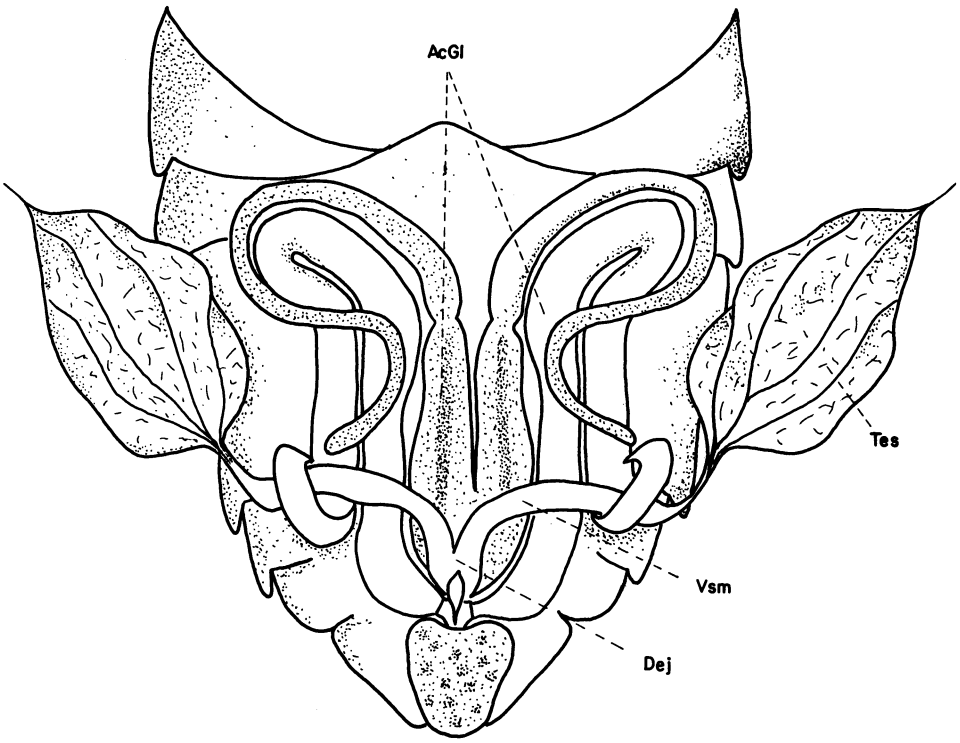


Fig. 6. Reproductive system of male *Lygus hesperus*. *Tes*, testis; *Vsm*, seminal vesicle; *Dej*, ejaculatory duct; *AcGl*, accessory glands. The medial pair of the accessory glands is shaded. (Dorsal view)

testes, but the rest of the system is wanting.

In adult males, 1 day old, the testes were large, puffed and firm, and the individual testicular tubules were readily apparent. The seminal vesicles were not developed, but small accessory glands were observable, having visible loops which curled around the undeveloped seminal vesicle.

Males 2–3 days old possessed accessory glands that were fairly large in relation to a sexually mature individual, but they appeared hollow and thin-walled. The seminal vesicles were beginning to enlarge but after examining stained slide preparations no sperm were located within these organs.

Males 3–5 days old had accessory glands which were beginning to fill basally with a white granular fluid. The seminal vesicle was partially filled with white fluid, which was shown to contain tightly packed sperm. These sperm averaged 1,142 microns in length.

The testes of males 5–6 days old were firm and pale-green. The seminal vesicles, although not completely full, were swollen and white. The accessory glands were distended, rigid, and also filled with white fluid.

From these observations it was obvious that sexual aggressiveness in the male (which usually begins at 5 days) is correlated with development of the accessory glands, not the testes. We did not determine if aggressiveness was dependent upon only the accessory glands, or on maturation of the seminal vesicle.

Females. The female reproductive system of *L. hesperus* is similar to that of *L. lineolaris* (Davis, 1955) and is shown in figures 7 and 8. It consists of a pair of ovaries joined medially to a

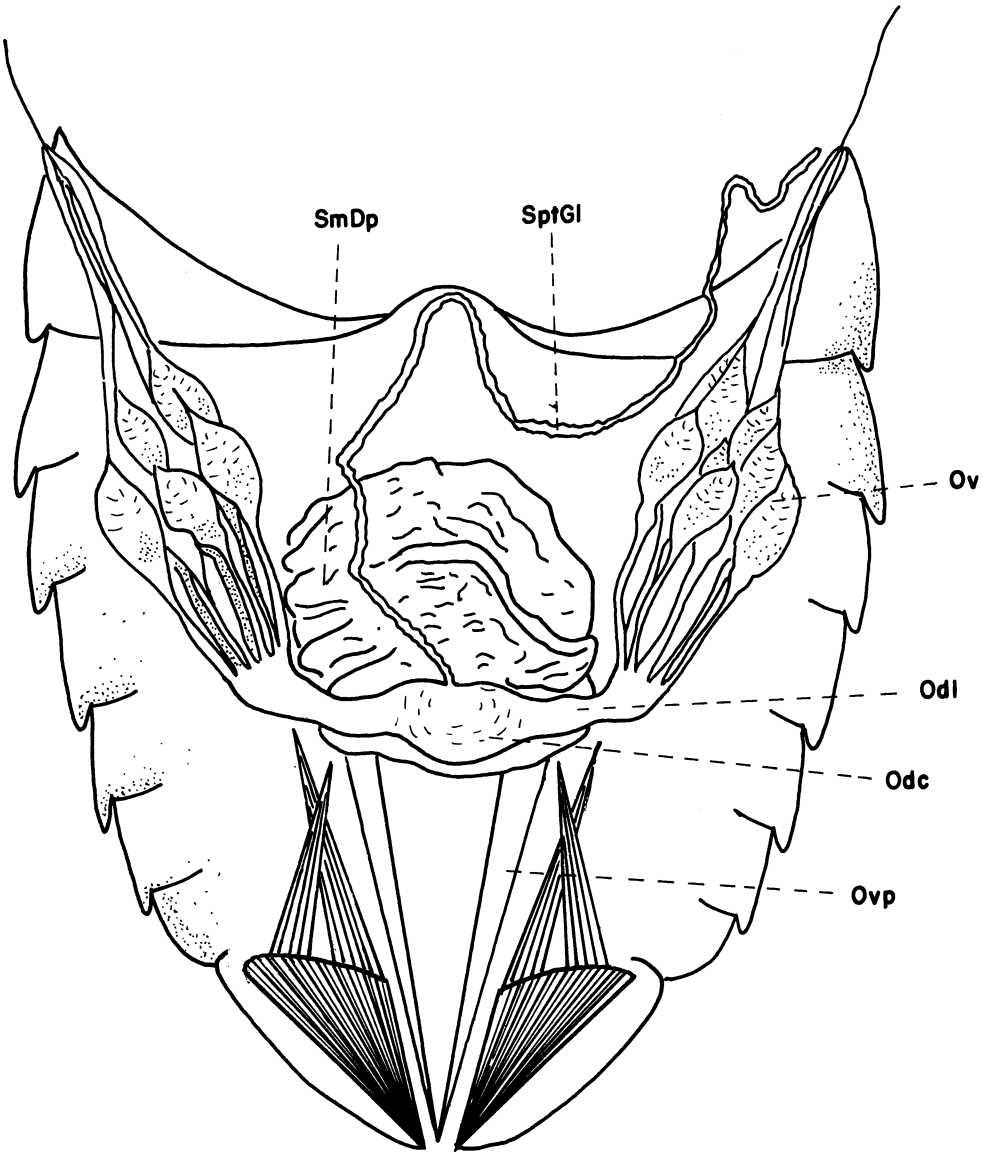


Fig. 7. Dorsal view of the reproductive system of a virgin female *Lygus hesperus*. The seminal depository (*SmDp*) is shown in the shriveled state. *SptGl*, spermathecal gland; *Ov*, ovary; *Odl*, lateral oviduct; *Odc*, common oviduct; *Ovp*, portion of the ovipositor.

common oviduct, called the genital chamber (Davis, 1955). Associated with the ovaries is a spermatheca, whose function is unknown, and a seminal depository which receives the sperm during copulation.

In contrast to the male, whose gonads are fully developed at the adult molt, the newly molted female has completely undeveloped ovaries. In a mature female, each ovary consists of seven ovarioles. Histological sections by Hussein (1966) revealed that the distal portion of each ovariole (called the egg tube)

is differentiated anteriorly into the germarium which contains the trophocytes, oogonia and young oocytes. The posterior region, known as the vitellarium, is where the oocytes mature into eggs, which are retained in a fully developed state in the apical portion of the ovariole before being oviposited.

Ovaries dissected from 1-day old adult females were atrophied. Trophocytes were present, but no oocytes. The vitellaria of 2-day old adult females were evident and contained the first visible oocytes. At 3 days of age the successive addition of growing oocytes divided the vitellaria into a series of egg chambers or follicles, which became progressively larger toward the more posterior region of the egg tube.

Adult females 5–7 days old invariably possessed 1–2 mature eggs in each ovariole plus oocytes of different ages which decreased in size toward the germarium. In all dissected virginal bugs, the seminal depository was shriveled and flattened. The seminal depositories in females which had just mated were always inflated, smooth surfaced, and appeared white. This organ in the inflated condition could be observed in living bugs through the 5–6 abdominal sternites and provided a means of determining the percentage of field-collected bugs which had mated, and also offered a limited means of determining the age of field-collected females.

In addition to the seminal depository, *L. hesperus* females have a bulbous organ which appears in unmated individuals to be the dorsal portion of the genital chamber. We have termed this structure the genital pouch. In newly mated females the genital pouch is greatly enlarged (see figure 8) but gradually decreases in size as time passes after mating.

Groups of ten females were dissected daily after mating, to determine the change in the condition of the genital pouch with time. The relative size of the genital pouch was assigned an arbitrary number to indicate its degree of distension; 1 indicated a pouch filled with fluid, 4 signified an empty one. The results, shown histographically in figure 9, show that immediately after mating the genital pouch was fully distended, but 5 days after copulation it was empty in 90 per cent of the females examined. Davis (1955) makes no mention of this structure, and would have failed to observe it unless he happened to dissect a specimen which has just mated. The significance of the structure at present is questionable, but it is believed to play a part in sperm transfer, as described below.

The seminal depository is composed of two portions, a center region and a lateral portion (Davis, 1955). Immediately after mating, motile sperm are found only in the center region. The sperm are present in the form of a compact, yellowish ball. An opaque fluid, similar in appearance to the fluid in the lateral pair of accessory glands of the male (which is quite different from the fluid of the medial pair) is present in the anterior-lateral portions of the seminal depository. The fluid which fills the genital pouch after mating is similar to that found only in the medial pair of male accessory glands. No sperm were found in the genital pouch.

Twenty-four hours after mating, the sperm ball in the seminal depository began to dissipate. At this time, however, the sperm were no longer motile. They appeared shortened, stiff and rod-like, without long tails. Dissection of females at 24-hour intervals after mating revealed that the sperm slowly migrated to the lateral portion of the seminal depository, and 5 days after mating the sperm were present throughout this organ.

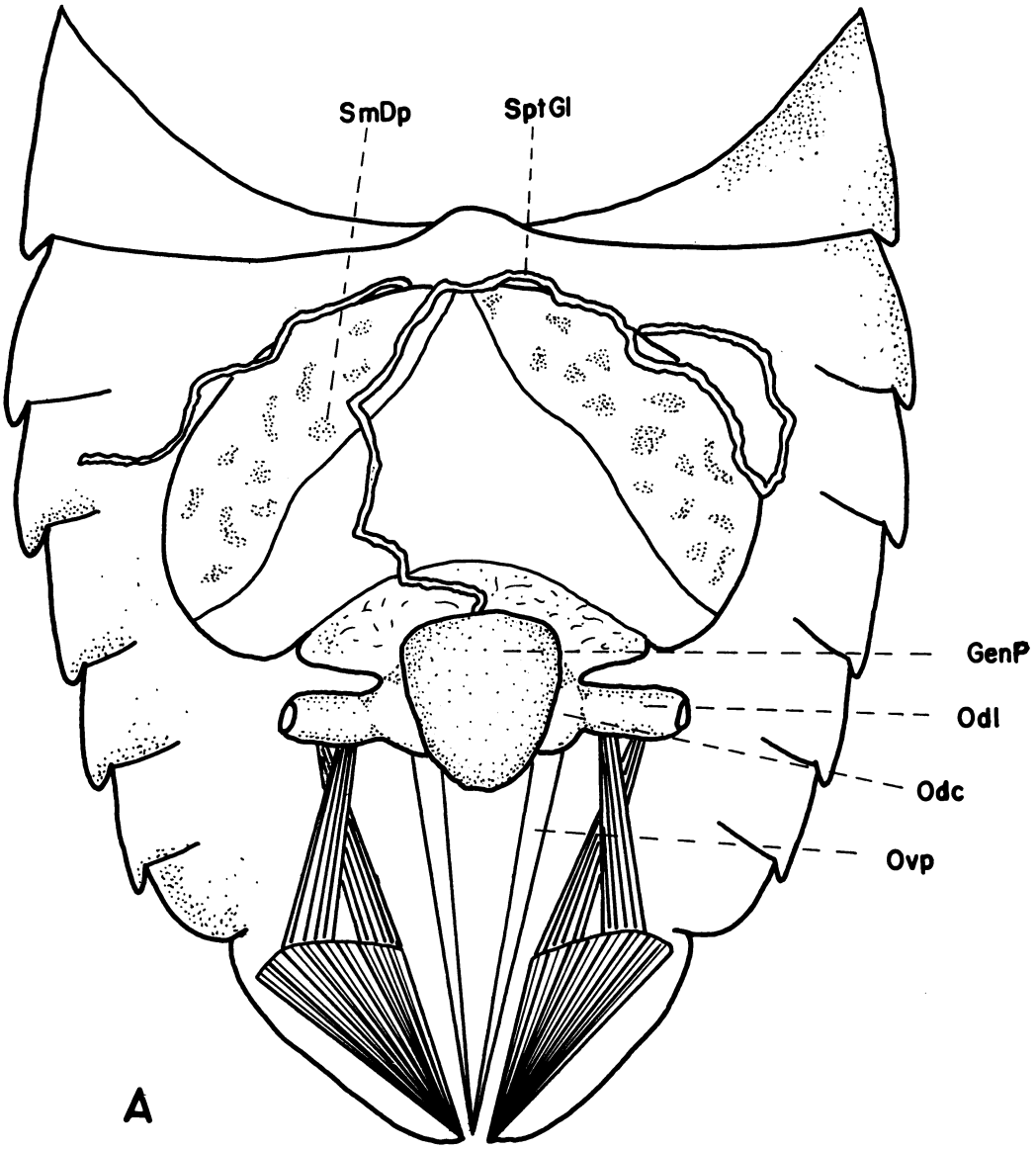
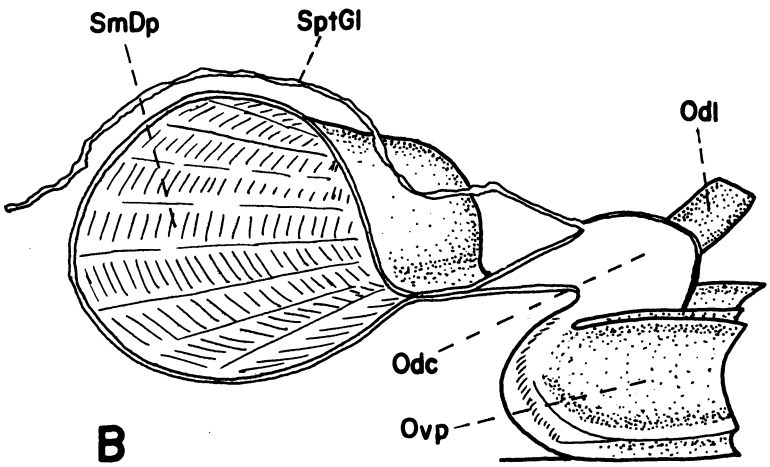
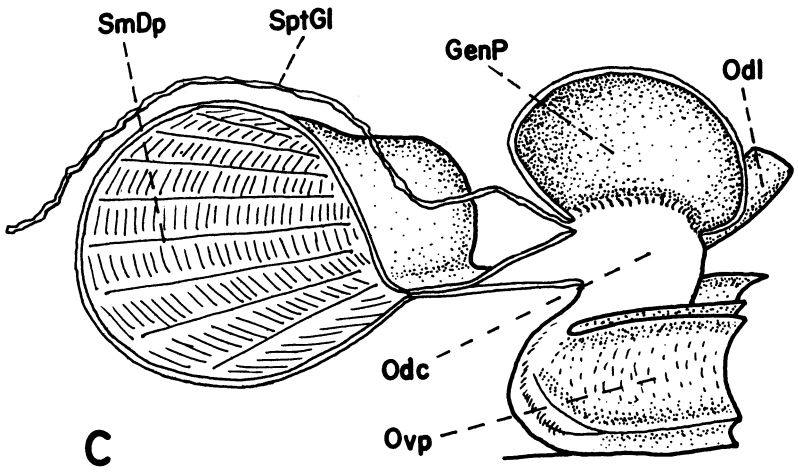


Fig. 8. Reproductive system of a mated female *Lygus hesperus*. A. Dorsal view showing the expanded seminal depository (*SmDp*) and inflated genital pouch (*GenP*) immediately after mating. B and C (opposite page). Median-lateral section showing the genital pouch immediately after mating (C) and 5 days later (B). Symbols are the same as in figure 7.





It is hypothesized that the mechanism for sperm transfer throughout the seminal depository involves emptying of fluid from the genital pouch. Also, the fact that females will not mate until 5 or 6 days after a previous mate, suggests an association between sperm transfer and receptiveness.

These observations suggest that female *L. hesperus,* which normally mate 5 days after becoming adults, coordinate their sexual receptiveness with maturation of first eggs. This dependency is not unequivocable, however, for in rare instances females dissected immediately after mating possessed only enlarged oocytes. More probably, sexual receptiveness is associated with production of the sex pheromone, and egg maturation has evolved to coincide with this time.

Fecundity records of mated and unmated females

At 80°F, female *L. hesperus* mature eggs and commence ovipositing about 9 days after becoming adults regardless of whether they are mated or not. Un-

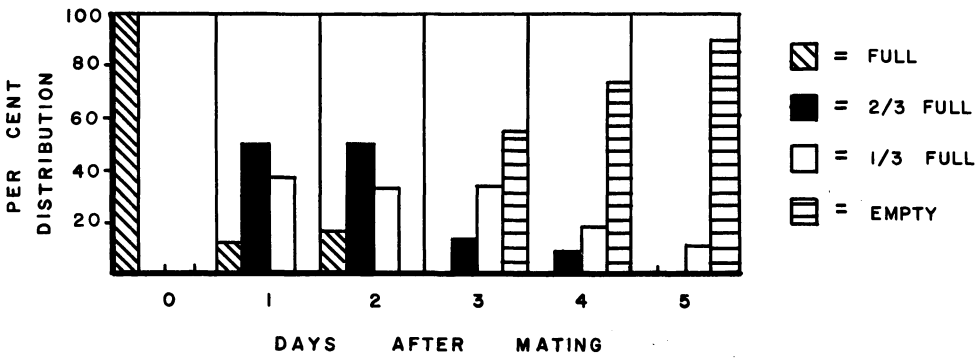


Fig. 9. Frequency distribution of the size of the genital pouch in relation to the number of days after mating.

mated females oviposit eggs which all fail to hatch. Studies in population dynamics require average daily ovipositional records and natural mortality data of the ovipositing females. Therefore, daily ovipositional records were maintained on 49 mated and 63 virgin females from the time of the imago molt until death. Longevity records were also maintained on both mated and virgin males.

The ovipositional records are summarized in table 5 and figure 10. Longevity of mated and virgin males averaged 49 and 46 days, respectively. Virgin females survived an average of 47 days but longevity of mated females was significantly ($P = 0.01$) shorter (38 days) than that of the virgins.

The average preoviposition period was 9.2 days (at 80°F) for both mated and virgin females. The mated females laid more eggs (but not significantly more) than the virgins (178.5 ± 82.2 vs. 154.6 ± 79.9). There was a significant difference in the number of egg-laying days; 26.4 days for mated females and 34.4 days for virgins. Both mated and virgin females, however, were able to lay eggs for about 70 per cent of their total adult life.

In attempting to understand the inherent ability of an insect to increase its numbers, the shape of the egg-laying curve in relation to the survival of the mothers is of paramount importance. Figure 10 reveals that, disregarding the daily irregularities, the egg-laying pattern is fundamentally triangular. The apex occurs when 100 per cent of the

TABLE 5
LONGEVITY AND OVIPOSITION DATA FOR MATED AND VIRGIN *L. HESPERUS*

Sex		Individuals tested	Adult longevity		Egg laying days		Total egg production	
			Mean	Range	Mean	Range	Mean	Range
			days		*days*		*eggs*	
Males	Mated.....	49	49.2	17–64	—	—	—	—
	Virgins.....	54	46.5	13–64	—	—	—	—
Females	Mated.....	49	38.0	19–64	26.4	5–55	178	13–382
	Virgins.....	63	47.0	27–64	34.4	3–60	154	4–332

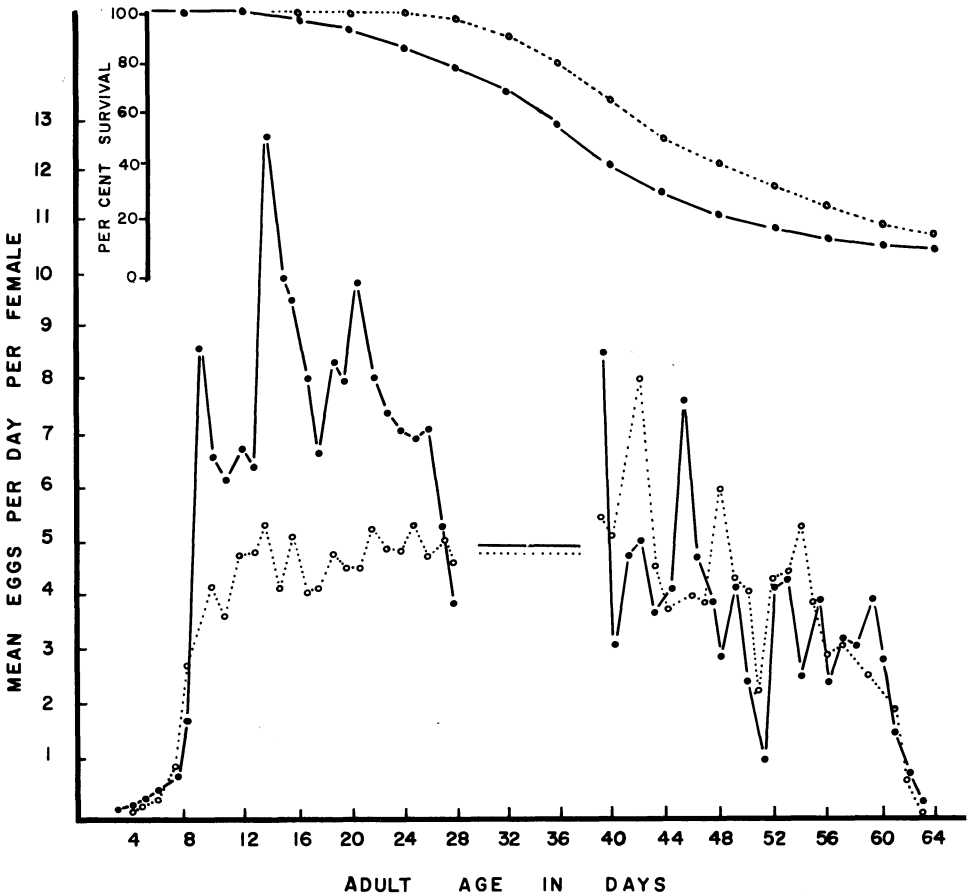


Fig. 10. Egg-laying curve and survival of female *Lygus hesperus*. Solid line: mated females. Dotted line: virgin females. The experiment was started with 49 mated and 63 virgin females. The short straight line in the center of the curve signifies that daily records were not maintained during that week.

females are still alive; fewer eggs are laid by a decreasing number of survivors as time passes. The significance of figure 10 is that it shows the contribution to the population by mothers of various ages. Mothers 45–55 days old, for example, contribute an insignificant number of offspring to the population because they represent only a small fraction of the original number of females.

Using population growth equations (Birch, 1948; Laughlin, 1965; Slobodkin, 1961), we calculated that, in our experiments, R_o (the net reproductive capacity) of *L. hesperus* was 41, and that under our laboratory conditions, r_m (the intrinsic rate of increase), was 0.1045 (see table 6). If a stable-aged distribution is permitted to mature in the laboratory, the contribution to R_o (or the population increase) by females 45 days or older is only three offspring, whereas 64 new members are added to the population by a mother less than 20 days old.

Although population statistics and mortality data obtained in the laboratory are not directly applicable to field populations, they indicate the upper limits below which the population operates. This is so because laboratory data are generated in the absence of predation, parasitism, inter- or intra-

TABLE 6

POPULATION STATISTICS DERIVED FROM COMPUTER-SIMULATED *LYGUS* POPULATIONS

Assumed nymphal survival	R_o*	r_m†	r_c‡	T_c¶
per cent				
100	95.559	.13050	.0506	45.05
73	67.086	.12150	.0465	45.13
43	41.317	.10451	.0400	46.86
30	27.695	.09802	.0368	45.15
10	9.281	.06966	.0491	45.33
8	7.386	.06406	.0443	45.15
6	5.546	.05695	.0379	45.10
4	3.698	.04685	.0290	45.14
2	1.847	.03126	.0136	45.14
1	0.955	——	-.0010	45.11
.5	0.461	——	-.0171	45.14

* $R_o = \int_o^\infty l_x m_x dx$ = ratio of female births in two successive generations (Birch, 1948).

† r_m = the intrinsic rate of natural increase, calculated from $\sum_a^w \frac{Vx}{e^{r_m \cdot x}} = 1$ (Laughlin, 1965).

‡ $r_c = \log_e R_o/T_c$ = capacity for increase.

¶ T_c = generation time.

specific competition, and in the presence of unlimited food and ovipositional sites, and optimum "weather."

Turning now to factors responsible for the growth of lygus field populations, we see that the reproductive biology of *L. hesperus* is aptly suited to insure population maintenance and increase. Lygus bugs, like most agricultural pests, begin each year anew through a series of colonizing episodes. Lewontin (1965) states that "colonization is the establishment of a population of species in a geographical or ecological [sic] space not occupied by that species." In other words, the absence of population pressure characterizes a colonizing episode. Thus, when lygus colonize, population pressure is absent because 1) the number of overwintering bugs is exceedingly low and 2) agricultural practices continually shift the geographical and ecological space required for established populations. The ability of the spring nymphs to provide for future growth of the population is dependent on field-mortality factors. Data concerning these factors are not available. Consequently, population statistics based on laboratory data were used to estimate the maximum permissible nymphal mortality that would enable the field population to continue to increase. This was done as follows:

During the past two years 43 per cent of all nymphs reared on beans survived to adults. This information plus the fecundity data presented in figure 10 was used to construct an initial life table.

This life table, which is presumably a realistic representation of lygus reproduction in our laboratory cultures, was used as a basis to simulate lygus populations and prepare additional life tables assuming various nymphal mortalities. In each of the simulated populations the adult mortality and fecundity data from figure 10 was used, and only the nymphal mortality was varied. The results of these studies are shown in table 6.

For a population to maintain itself, the net reproductive capacity (R_o) must be at least 1.000. Table 6 shows that almost 99 per cent of all nymphs (and eggs) may die and the population will still maintain an R_o of 1.0.

Butler (1968) conducted an extensive

series of regression analyses of *L. hesperus* populations on time in numerous alfalfa fields in southern Arizona. His results show that during the summer, over a ten-year period, the regression coefficient (b) was 0.0172, which, according to Butler's graphs, is equivalent to a ten-fold increase every 56 days. Fifty-six days under Arizona temperatures conditions are equivalent to 1.23 generations; thus, a net increase of eight times presumably occurred in one generation. Our population simulation studies indicate then, that under the Arizona conditions, the nymphal mortality would be about 92 per cent.

PART II. FIELD BIOLOGY OF *LYGUS HESPERUS* SEX PHEROMONE[3]

Chemical communication between animals is a well documented phenomenon (Marler and Hamilton, 1966). In recent years, insect pheromones have received much attention (Jacobson, 1966). Sex attractants, which constitute a large proportion of the known insect pheromones, have been most thoroughly investigated in holometabolous insects, especially Lepidoptera, with reports of attractants in more than 110 species (Jacobson, 1965). Among the hemimetabolous insects, however, less than a dozen species have been investigated. Doane (1966) was the first to report a sex attractant in Homoptera (the red pine scale, *Matsucoccus resinosae* Bean and Godwin). Subsequent reports demonstrated sex pheromones in the red scale, *Aonidiella aurantii* (Maskell) (Tashiro and Chambers, 1967) and the citrus mealybug *Planococcus citri* (Risso) (Gravitz and Willson, (1968).

The first experimental evidence for a sex pheromone in Hemiptera was published by Scales (1968), when he demonstrated that virgin females of the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), attracted males. During June and July, 1966, at Shafter, the existence of a sex pheromone in *Lygus hesperus* was preliminarily demonstrated. In 26 trapping days a total of 46 males was captured, all in the traps baited with virgin females. No males or females were caught in traps baited with other males, or with beans alone. On the basis of this preliminary experiment, the studies reported herein were initiated at Davis in early 1968.

Methods and Materials

The bugs used in this study were reared collectively or on pallets. Adult bugs less than 24 hours old were placed in the traps for bait. Generally, virgins were used, but occasionally field-collected bugs were tested. Green beans changed twice weekly were always present in all traps regardless of whether bugs were present or not.

The body of the trap, shown in figure 11, was constructed from a half-gallon ice cream carton. Both ends of this carton were fitted with removable funnels made from 16-mesh aluminum window screening; the screen funnels pointed toward the trap's center. The insects used as bait were housed in a half-pint carton, the bottom of which was replaced with screen and the top with a removable screen to permit replacing bugs or beans. A hole the size of the half-pint carton was cut in the side of the large carton, and the small carton which would house bait insects was glued in place. The inner surface of the large container was coated with "Stikem

[3] Taken in part from a thesis submitted in February, 1969, by P. R. Hughes to the Graduate Division, University of California, Davis, in partial fulfillment of the requirements for the Master of Science degree.

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