Modeling of Soybean Pod Feeding Behavior of Stink Bugs¹

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(Received February 20, 1987)

The feeding behavior of the adults on soybean pods was observed for four stink bug species, *Halyomorpha mista* UHLER (Pentatomidae), *Riptortus clavatus* THUNBERG (Alydidae), *Nezara antennata* SCOTT (Pentatomidae) and *Piezodorus hybneri* GMELIN (Pentatomidae) in the laboratory. The feeding duration and frequency per day were examined for each species. An exponential distribution was fitted to the observed frequency distribution of feeding duration. The insects randomly selected beans for feeding irrespective of the bean size and injury history of the bean except for the small and severely injured bean. The distribution of the total feeding duration per bean was expressed by a compound Poisson distribution. These mathematical models described the relationship between the insect density and bean damage.

INTRODUCTION

The injury analysis is a key component in setting dynamic economic injury level (EIL). To forecast the yield loss dynamically the three processes must be understood—crop growth and compensation, pest population dynamics, and the pattern of injuring crops by pests. Integrated studies with such scope are scarce even though these are needed in a sound integrated pest management program (IPM). GUTIERREZ and his colleagues (GUTIERREZ et al., 1975; WANG et al., 1977; WILSON et al., 1980; WILSON and GUTIERREZ, 1980) developed such models by coupling the cotton growth model with injury models describing the insect attacks. Categorization and quantification of pest damages to crops are necessary to incorporate the pest damages in crop growth simulators to predict yield reductions (BOOTE et al., 1983).

Insect pests of soybean seed are divided into two major groups, chewers with biting-chewing mouth parts and suckers with piercing-sucking mouth parts. The effects of seed chewers e.g. pod borers, on yield were examined by artificial depodding (KINCADE et al., 1971; SMITH and BASS, 1972; THOMAS et al., 1974 a), whereas the effects of seed suckers e.g. stink bugs, on yield remains to be examined by some artificial devices. Some researchers (YEARGAN, 1977; TODD and TURNIPSEED, 1974; THOMAS et al., 1974 b) analyzed the effect of stink bug density on soybean yield by releasing stink bug populations on caged soybeans. In their work, however, the feeding process of stink bugs

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and their potential infestation ability were not quantified.

In this paper, the feeding behavior of different species of stink bugs on soybean is analyzed and simulated by mathematical models. Also, the relationships of the amount of injury with pest species, population density, and the growth stage of soybean were described by an analytical model.

MATERIALS AND METHODS

Adult males and females of *Halyomorpha mista* UHLER (Pentatomidae), *Riptortus clavatus* THUNBERG (the bean bug) (Alydidae), *Nezara antennata* SCOTT (the oriental green stink bug) (Pentatomidae) and *Piezodorus hybneri* GMELIN (Pentatomidae) were collected during 10–20th September 1980 from a soybean field at the National Institute of Agro-Environmental Sciences (NIAES), Tsukuba. Most of them were newly emerged and used after 2–4 days of collection for observation of feeding behavior. Since no individuals oviposited during and after experiment, they were thought to be in a state of reproductive diapause.

Soybean varieties of Kakushin 1 and Norin 2 were sown on 18th June 1980. From these soybean fields, beans used for experiments were collected and were divided into five size grades by their live (fresh) weight (I, <0.1 g; II, 0.1–0.2 g; III, 0.2–0.4 g; IV, 0.4–0.6 g; V, >0.6 g). Each group was again divided into two categories, uninjured and injured (sucked). The beans damaged by agents other than the stink bugs were excluded from the experimental materials. The beans were offered to the bugs with or without the pod shells. In Expts. 1–4, the feeding behavior was observed in the laboratory at room temperatures of 15–28°C and under a day length of 13 hr (5:00–18:00).

Expt. 1. Daily rhythm and duration of feeding. Adults of each species and sex were individually kept with four soybean pods in a glass tube (23 cm in length and 4 cm in diameter). Each pod contained two beans of grades III–IV. Four types of behavior, viz., feeding (the stylet piercing deeply into the bean), probing (exploration with the stylet piercing through the pod shell or a bean), resting and walking were observed and recorded during 2-day periods. The observations were made every 15 min during the first 2 hr after the initiation of experiment (started at 14:00 for *H. mista* and 9:00 for the other three species) and thereafter every 30 min until 24:00 and every hour from 24:00 to 6:00. The numbers of individuals used were shown in Table 1.

Expt. 2. Effect of insect density on feeding duration. The soybean plants had been artificially defoliated before experiment and the only main stem with four nodes holding 3–5 pods per node was offered to stink bugs. Each pod contained mostly two beans but ranged 1–4 ones per pod. Females of *H. mista* were released at densities of 1, 2, 3 and 4 females per plant. Feeding behavior was observed for one day, to determine frequency and duration of feedings.

Expt. 3. Effect of bean quality on feeding behavior. Females of *H. mista* were individually placed in a small petri dish (2 cm in height, 9 cm in inside diameter) with two uninjured and two moderately injured beans of size grades III (small) and IV (large) on filter paper. The injured and the uninjured beans were placed alternatively. The frequency of feedings and duration of feeding were recorded for each bean for 2 days. Ten individuals were observed for each size grade of beans.

Expt. 4. Feeding time capacity of a bean. The capacity of a bean to be sucked or the

Fig. 1. The feeding behavior of female bugs on soybean in *H. mista* (A), *R. clavatus* (B), *N. antennata* (C) and *P. hybneri* (D). Shaded rectangles and open ones indicate the feeding behavior and the behavior including probing, walking and resting, respectively.

Table 1. The behavioral characteristics of adult stink bugs on soybean

Species	Sex	No. obs.	Daily feeding time hr/day (S.E.)	Feeding frequency feedings/day (S.E.)	Duration of a feeding hr/feeding (S.E.)
<i>Halyomorpha</i>	f	10	6.20 (0.58) a	3.65 (0.50) de	1.70 (0.21) f
<i>mista</i>	m	7	5.39 (0.90) a	2.71 (0.66) de	1.99 (0.30) fg
<i>Riptortus</i>	f	10	5.36 (0.97) a	2.65 (0.32) d	2.02 (0.23) fg
<i>clavatus</i>	m	2	8.50 (0.00) ab	4.00 (1.00) de	2.13 (0.43) fgh
<i>Nezara</i>	f	10	11.29 (1.57) b	3.80 (0.98) de	2.97 (0.25) hi
<i>antennata</i>	m	3	16.17 (4.42) c	4.00 (0.58) de	4.04 (1.07) i
<i>Piezodorus</i>	f	8	10.52 (0.88) b	3.94 (0.33) de	2.67 (0.25) gh
<i>hybneri</i>	m	4	13.00 (1.84) bc	4.50 (1.26) e	2.89 (0.40) ghi

The results of ANOVA were shown by alphabets, a-i, of which each same letter indicates the values without significant differences at 5% level from multiple comparisons among pairs of means by T-method. Standard errors of means were independently calculated before ANOVA.

feeding time capacity was expressed in terms of the duration of time (hr) required to be entirely consumed by an adult of *H. mista*. An adult of *H. mista* was introduced into a small petri dish with a bean and was allowed to feed the bean up to 1 hr. The proportion of sucked tissue to the total volume was determined by dissecting the bean. The feeding time capacity of the bean for each size grade of beans was calculated from the sucked proportion.

RESULTS

Daily rhythm and duration of feeding

The feeding behavior observed in Expt. 1 was shown only for females of each species in Fig. 1, in which feeding was indicated by shaded boxes and probing, walking and

Fig. 2. Comparison of the cumulative frequency distributions of feeding duration between observed (step lines) and calculated ones (curves) based on Eq. (1) with $b=0.588$ for *H. mista* (A), $b=0.495$ for *R. clavatus* (B), $b=0.337$ for *N. antennata* (C) and $b=0.375$ for *P. hybneri* (D).

resting by open ones. No difference in daily rhythm of feeding was observed between the sexes for all the species examined.

The mean time spent for each feeding and the total feeding time per day were shown in Table 1. *N. antennata* and *P. hybneri* spent about one-half day for feeding while *H. mista* and *R. clavatus* spent less than a quarter of a day. There was no significant difference in the total feeding time between the sexes for all the species. The number of beans attacked per day increased with an increase in the total feeding time and with a decrease in the duration of feeding time. Therefore species such as *P. hybneri* that has a greater total feeding time and a shorter feeding duration, attacks a greater number of beans than another species such as *R. clavatus*.

The duration of feeding behavior was greatly variable with a maximum of nearly 10 hr (Fig. 1). The frequency distribution of feeding durations observed during 2 days in Expt. 1 was rearranged in a cumulative frequency distribution curve. The cumulative frequency distribution for the female of each species is shown in Fig. 2. The exponential distribution with a mean duration of t_{mean} (hr) was fitted to the observed frequency distribution. Its cumulative distribution function $F(x)$ and density function $f(x)$ are, letting $b=1/t_{\text{mean}}$,

$$\begin{aligned} F(x) &= 1 - \exp(-bx), \\ f(x) &= b \exp(-bx), \end{aligned} \quad (1)$$

where the parameter, b , is the instantaneous rate of feeding termination. $F(x)$ represents the probability that the duration of a feeding, X (hr), is shorter than or equal to x (hr), $F(x) = \text{Prob}(X \leq x)$. This equation was fitted to all species and sexes, with the value of b specific to each species.

Effect of insect density on feeding duration

Disruption of feeding behavior by other individuals was observed in *H. mista* in

Table 2. Effect of density on feeding behavior of female *Halyomorpha mista*

Density	No. obs.	Daily feeding time hr/day (S.E.)	Feeding frequency feedings/day (S.E.)	Feeding duration hr/feeding (S.E.)
1	6	11.42 (2.17)	4.33 (0.67)	2.63 (0.53)
2	8	12.84 (1.61)	4.88 (0.67)	2.63 (0.38)
3	6	11.21 (1.05)	3.83 (0.40)	2.92 (0.36)
4	8	9.53 (1.59)	4.25 (0.70)	2.24 (0.33)
Result of ANOVA		n. s.	n. s.	n. s.

Table 3. The distribution of feeding frequency among eight beans for *H. mista* female

Total feedings	Number of beans (observed/expected)					Kolm. test	
	0	Frequency of feeding trace				d	Sig. level
		1	2	3	4+		
4	5/4.69	2/2.68	1/0.57	0/0.05	0/0.00	.046	.85 ≤ <i>p</i>
4	5/4.69	2/2.68	1/0.57	0/0.05	0/0.00	.046	.85 ≤ <i>p</i>
9	2/2.41	5/3.09	0/1.77	0/0.59	1/0.15	.188	.42 ≤ <i>p</i>
11	1/1.84	5/2.89	1/2.07	0/0.89	1/0.31	.158	.53 ≤ <i>p</i>
5	4/4.10	3/2.93	1/0.84	0/0.12	0/0.01	.016	.95 ≤ <i>p</i>
3	6/5.36	1/2.30	1/0.33	0/0.02	0/0.00	.082	.55 ≤ <i>p</i>
7	3/3.14	3/3.14	2/1.35	0/0.32	0/0.05	.046	.92 ≤ <i>p</i>
8	2/2.75	4/3.14	2/1.57	0/0.45	0/0.09	.094	.78 ≤ <i>p</i>
11	1/1.84	5/2.89	0/2.07	2/0.89	0/0.31	.158	.53 ≤ <i>p</i>
11	4/1.84	1/2.89	1/2.07	0/0.89	2/0.31	.270	.21 ≤ <i>p</i>

Each observed distribution was compared with a binomial distribution of the same mean by a Kolmogorov test.

Table 4. Result of choice experiment of *H. mista* females

Bean size	No. of observed bugs	Bean quality	Feeding frequency			Duration of a feeding		
			feedings/ 2 days	Gaj.	level	hr/feeding (S.E.)	<i>F</i>	level
Small	10	injured	8	6.68	<i>p</i> < .01	1.19 (0.25)	7.42	<i>p</i> < .025
		uninj.	22			3.59 (0.52)		
Large	10	injured	20	1.65	n.s.	3.75 (0.87)	0.12	n.s.
		uninj.	29			3.41 (0.55)		

The feeding frequency was compared with a null hypothesis, 1: 1, by a G-test of goodness-of-fit, and duration of a feeding was tested by ANOVA.

Expt. 3. The feeding was often terminated when the other individual(s) walked nearby or began to feed on the same bean. When an adult of *H. mista* was placed alone, it left the plant 0.17 times per day. The leaving frequency ranged 0.25–0.38 times/day/insect when the adult density increased to 2–4 individuals/plant. However, daily feeding time, feeding frequency and feeding duration were not significantly different between densities (Table 2).

Choice of beans for feeding

The frequency distribution of feedings in terms of the bean was obtained from

Fig. 3. The feeding time capacity, C (hrs), of a bean in relation to its fresh weight.

Fig. 4. Calculated changes in distribution of bean quality as affected by the days exposed to attack for 1, 3, 5 and 7 days by *H. mista* (A), *R. clavatus* (B), *N. antennata* (C) and *P. hybneri* (D). The density is 40 bugs/1,000 beans, and the bean size expressed in terms of the feeding capacity, C , is 12 hr.

Expts. 1 and 2. An example of the distribution is shown in Table 3 for *H. mista* females in Expt. 2. When beans are attacked randomly by the insect, the frequency distribution of the number of feedings per bean becomes a binomial distribution. The observed frequency distribution was compared with the binomial distribution of the same mean. None of the observed distributions indicated significant differences from binomial distributions by a Kolmogorov goodness-of-fit test (CONOVER, 1972).

Effect of bean quality and quantity on feeding

In the choice experiment between injured and uninjured beans (Expt. 3), the frequencies of feeding throughout the 2-day experiment are shown in relation to bean conditions (Table 4). The frequencies were compared with null hypothesis of 1:1 by the method of G-test of goodness-of-fit (SOKAL and ROHLF, 1981). When insects were allowed to choose injured and uninjured beans of size grade IV, they chose beans randomly. Uninjured beans, however, were chosen more frequently than the injured among the smaller beans (size grade III).

The mean time spent for a feeding on a small injured bean was remarkably shorter than that on the small uninjured type. Among the large beans, however, the mean time on the injured bean was not different from that on the uninjured bean (Table 4). It means that the feeding behavior is not affected by the quality or quantity of the bean so long as a small amount of bean tissue is left uninjured.

The feeding time capacity of an uninjured bean increased linearly with increasing its fresh weight in Expt. 4 (Fig. 3). The following equation was fitted.

$$C = 39.36W - 1.34, \quad (2)$$

where C is the feeding time capacity (hr) and W is the fresh weight (g) of a bean.

ANALYTICAL MODEL

An analytical model was developed to describe the process of quality deterioration of beans due to attack of stink bugs. A soybean field was assumed being attacked for several days by an immigrated stink bug population. Beans were assumed to be randomly chosen at every feeding with an equal probability. The total frequency of feedings in a day (24 hr) was assumed to be constant for each species and sex. Based on these assumptions, the number of injured beans and their quality (the proportion of bean tissue left uninjured) were calculated.

Assuming the frequency of feedings per bean takes a Poisson distribution with a mean frequency of m , h_k , the probability that a bean is fed on k times, is given by

$$h_k = [\exp(-m)] m^k / k!. \quad (3)$$

The distribution of total feeding duration in terms of individual bean can be obtained as follows. Let $F^{k*}(x)$ be the probability that the sum of feeding durations of k times, $X_1 + X_2 + \dots + X_k$ (hr), is shorter than or equal to x (hr), $F^{k*}(x) = \text{Prob}(X_1 + X_2 + \dots + X_k \leq x)$, and $f^{k*}(x)$ be its density function. These functions are given by convolutions of $F(x)$ and $f(x)$ (FELLER, 1971),

$$F^{k*}(x) = 1 - \exp(-bx) \sum_{i=0}^{k-1} (bx)^i / i!,$$

$$f^{k*}(x) = b(bx)^{k-1} \exp(-bx) / (k-1)!$$

This distribution is known as a gamma distribution with the parameters b and k . The special case $k=1$ represents the exponential distribution expressed by Eq. (1). When $k=0$, it is defined as $F^{0*}(x) = 1$. The mean and variance of the sum of k time feeding durations are $E(X_1 + \dots + X_k) = kt_{\text{mean}}$ and $V(X_1 + \dots + X_k) = kt_{\text{mean}}^2$, respectively.

Let T be the total duration (hr) that a bean has been fed on by stink bugs, the probability $G(x)$ that a bean is fed on less than or equal to x (hr), $G(x) = \text{Prob}(T \leq x)$, is obtained as follows. $G(x) = (\text{probability that a bean is not fed on}) + (\text{probability that a bean is fed on once}) + (\text{probability that duration of a feeding is less than or equal to } x) + \dots + (\text{probability that a bean is fed on } k \text{ times}) + (\text{probability that a sum of feeding duration of } k \text{ times is less than or equal to } x) + \dots$. Then, $G(x)$ is given by

$$G(x) = \sum_{k=0}^{\infty} h_k F^{k*}(x)$$

$$= 1 - \exp(-m - bx) \sum_{k=1}^{\infty} m_k / k! \sum_{i=0}^{k-1} (bx)^i / i!, \quad (4)$$

$$G(0) = \exp(-m) \quad (5)$$

This distribution is one of the compound Poisson distributions. The probability that a bean is not injured at all is given by Eq.(5), which is identical with the h_0 of the previous Poisson distribution (Eq. (3)). With the values of parameters b and m , this distribution can be explicitly obtained by numerical calculation.

Although Eq. (4) has summations of series, its mean and variance can be obtained. Let $L(u)$ and $M(u)$ be the Laplace transforms of distributions $F(x)$ and $G(x)$, respectively, and $H(s)$ be the generating function of h_k . Then $M(u)$ is given as $M(u)=H(L(u))$ (FELLER, 1971). In our model,

$$\begin{aligned} L(u) &= \int_0^{\infty} \exp(-xu) f(x) dx \\ &= b/(u+b), \\ H(s) &= \sum_{k=0}^{\infty} s^k h_k \\ &= \exp(-m(1-s)), \end{aligned}$$

where the first lines of these equations represent the definition of Laplace transform and generating function, respectively. Let $g(x)$ be the density function of $G(x)$,

$$\begin{aligned} M(u) &= \int_0^{\infty} \exp(-xu) g(x) dx \\ &= H(L(u)) \\ &= \exp(-mu/(u+b)), \end{aligned}$$

where the first line of this equation represents the definition of Laplace transform. The mean and variance of T is given as,

$$\begin{aligned} E(T) &= \int_0^{\infty} x g(x) dx \\ &= -M'(0) \\ &= m/b \\ &= mt_{\text{mean}}, \end{aligned} \tag{6}$$

$$\begin{aligned} V(T) &= \int_0^{\infty} x^2 g(x) dx - E(T)^2 \\ &= M''(0) - M'(0)^2 \\ &= 2m/b^2 \\ &= 2mt_{\text{mean}}^2, \end{aligned} \tag{7}$$

where the first lines of these equations represent the definition of mean and variance of T , and $M'(u)$ and $M''(u)$ are the derived functions of first and second order of $M(u)$. It is reasonable that in Eq. (6) the expected total duration that a bean has been fed on, $E(T)$, is expressed by the product of the mean feeding frequency, m , and the mean feeding duration of a feeding, t_{mean} . The variance of the total feeding duration, $V(T)$ in Eq. (7), is equal to $2mt_{\text{mean}}^2$, two times of the product of m and the square of t_{mean} , which is the variance of the duration of a feeding.

The quality of a bean was assumed to be expressed by the proportion of tissue left uninjured as $1 - T/C$, where T is the total duration (hr) of feedings and C is the feeding time capacity (hr) in Eq. (2). This equation was also assumed to hold for all species. The following values are necessary for calculation of the quality distribution of beans: the number of bugs, the duration exposed to bugs in days, the daily feeding frequency of a bug, the mean duration of a feeding, the size (expressed by C) and number of beans. These values were assumed to remain constant for several days during which the beans were exposed to a stink bug population. Then the change in distribution of the quality of beans were calculated with Eq. (4).

Fig. 5. The calculated relationships between bug density and the percentage of injured beans after 2- and 7-day infestation (A) and between bug density and mean quality of beans for bean sizes of $C=8$ and 24 hr (B).

An example was shown in Fig. 4. The proportion of uninjured beans decreases progressively. Among injured beans, the proportion of heavily injured beans becomes high as feeding is repeated. Stink bugs may avoid feeding on such beans of low quality under natural conditions. Thus the proportion of uninjured beans would be lower than the calculated.

The proportion of injured beans increased as the density of bugs increased (Fig. 5 A). The number of injured beans due to *R. clavatus* was smaller than that due to the other three species with comparable density. The deterioration of bean quality due to *N. antennata* and *P. hybneri* was appeared to be more serious than that due to *H. mista* and *R. clavatus* (Fig. 5 B).

DISCUSSION

Light field infestation of beans by stink bugs results in a higher proportion of lightly injured beans than those of moderately or heavily injured ones as shown in the case of *Nezara viridula* LINNÉ (southern green stink bug) (NILAKHE et al., 1981 a, b, c) and *Acrosternum hilare* SAY (green stink bug) (YEARGAN et al., 1977). Our model also predicted that as the total amount of injury increased, the proportion of uninjured beans decreased and that of the heavily injured increased.

Our observation on feeding selection of beans agrees with that of KOMORI and TAKAI (1982) who showed that the frequency distribution of the number of sucking points on maize grains due to *N. antennata* fitted to a truncated Poisson distribution. When beans were not severely damaged, the stink bug seemed to select beans for feeding at random.

If only the intact crop has high commercial value, infestation of stink bug species with high feeding frequency is economically important. Both *N. antennata* and *P. hybneri* have not only a greater total duration of feeding per day, but also a higher

feeding frequency per day. These species, therefore, are regarded as the potential pests of economic importance.

In our model, only the two parameters, m (mean feeding frequency per bean) and b (inverse of mean feeding duration) in Eq. 4, determine the frequency distribution of bean quality. These two parameters are obtained from the following three sources of information: the size and number of beans exposed to the infestation, the duration and frequency of feedings of the insect, the number of bugs and the duration of infestation. The last category, i.e. the product of (number of bugs) and (duration of infestation), is known as "insect-day". When the feeding behavior is independent of both the pest density and the bean history of damage, the "insect-day" index will be useful for the short term evaluation of damage of crops. For long term evaluation, however, it is necessary to incorporate the dynamics of pest population, the growth and compensation of crops and the interactions between pests and crops into the integrated study of damage analysis.

ACKNOWLEDGEMENTS

The authors thank Drs. S. MIYAI and T. MIWA, NIAES, for their valuable advice of analysis and modeling and Prof. E. KUNO and Dr. H. INOUE, Kyoto University, and Dr. R. N. SINHA, Agriculture Canada Winnipeg Research Station for reading the manuscript.

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