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Author(s): S. M. Greenberg, T. W. Sappington, D. W. Spurgeon, and M. Sétamou

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Boll Weevil (Coleoptera: Curculionidae) Feeding and Reproduction as Functions of Cotton Square Availability

S. M. GREENBERG,¹ T. W. SAPPINGTON,² D. W. SPURGEON,³ AND M. SÉTAMOU⁴

Integrated Farming and Natural Resources Research Unit, Kika de la Garza Subtropical Agricultural Research Center, 2413 East Highway 83, Weslaco, TX 78596

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ABSTRACT The influence of food item availability on boll weevil, *Anthonomus grandis grandis* Boheman, feeding and reproduction was determined by providing different numbers of cotton squares (flower buds) to individual weevils. Squares were replaced daily after a 5-d feeding and mating conditioning period. The number of lifetime punctures produced by boll weevil females and males increased with square availability. The total number of punctures caused by boll weevil females was 2.7-fold higher than that caused by males. Fecundity was significantly higher in the 10:1, 15:1, and 20:1 (squares:female) treatments than in the 1:1 treatment. The relationship between eggs laid per day and the square to female ratio significantly changed over the life of the female, with the largest differences among treatments occurring in the first 3 wk of adulthood. Survival of weevil progeny to adulthood was about two-fold higher in the 10:1, 15:1, and 20:1 treatments than in the 1:1 and 5:1 treatments. When each boll weevil female was provided 10, 15, or 20 cotton squares per day, estimates of a population growth index (percent of immatures surviving to adulthood divided by immature development time) and the exponential rate of increase (r_m) were significantly higher than for those provided only one or five squares per day. Boll weevil populations maintained at a square:weevil ratio of 10:1 or above will increase >60-fold each generation (R_0), a rate significantly higher than that exhibited under 5:1 or 1:1 square:female regimens. These data show that daily provision of 10 squares per female provides sufficient resources to elicit a maximal oviposition response in the laboratory. Our results also will be useful in predicting changes in boll weevil populations relative to crop phenology and starting population density.

KEY WORDS boll weevil, feeding, oviposition, growth and reproductive indices, cotton

THE BOLL WEEVIL, *Anthonomus grandis grandis* Boheman, remains a key pest of cotton (*Gossypium hirsutum* L.) in areas of the U.S. cotton belt from which it has not been eradicated. The female boll weevil feeds and oviposits primarily in the flower buds (squares) of cotton. Understanding the effects of host plant availability on feeding and oviposition behavior is of particular importance in evaluating the potential for population growth and crop injury by the boll weevil. Bottrell (1976) indicated that the reproductive potential of field populations of the boll weevil was highly variable, and he presumed that large populations limited further population growth by reducing

available oviposition sites. Sterling and Adkisson (1978) also reported a density-dependent relationship between boll weevil population level and subsequent population growth. These authors concluded that the carrying capacity of a cotton field for boll weevils was dependent on square availability. However, it cannot be determined from these reports if reduced square availability limits population growth through reductions in the survival rates of larvae in squares containing multiple eggs or if oviposition rates of adults also are reduced.

Preliminary studies have indicated that limited square availability can influence reproductive development of the female weevil (Spurgeon and Raulston 1997). However, available estimates of oviposition or fecundity from laboratory studies have either omitted useful descriptions of the sizes and numbers of cotton squares provided to weevils (Cushman 1911, Isley 1928, Cole and Adkisson 1982) or if the number of squares provided were less than the average daily production of eggs (Lambert et al. 1979, Roach 1979) and thus may have been limiting. Our objectives were to gain additional insight into the influences of square

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¹ E-mail: sgreenberg@weslaco.ars.usda.gov.

² Current address: USDA-ARS, Corn Insect and Crop Genetics Research Unit, Genetic Bldg, C/O Insectary Iowa State University, Ames, IA 50011.

³ Areawide Pest Management Research Unit, Southern Plains Agricultural Research Center ARS-USDA, College Station, TX 77845.

⁴ Texas Agricultural Experimental Station, Texas A&M University System, Weslaco, TX 78596.

availability on potential population growth by examining the rates at which feeding and oviposition punctures are produced, and the survival of offspring in response to discrete levels of square availability.

Materials and Methods

Boll Weevil Culture and Cotton Squares. Adult boll weevils were reared from field-collected infested squares. Approximately 1,000 infested squares were collected from the ground in cotton fields in the Lower Rio Grande Valley of Texas in June 2000. Squares were carefully dissected, and those with live third instars were closed back up and held within screen cages in an environmental chamber at $27 \pm 1^\circ\text{C}$, 65% RH, and a photoperiod of 14:10 (L:D) h. Temperature and humidity were monitored by a Fisher-brand Traceable Relative Humidity Meter with temperature readout (Fisher Cat. No. 11-661-12, Control Company, Friendswood, TX). After completion of larval development, pupae were harvested from squares and placed in 9-cm diameter petri dishes (five per petri dish) containing a shallow layer of moist vermiculite. Pupae were examined daily until adult eclosion. On the day of eclosion, adults were sexed using the method of Sappington and Spurgeon (2000), weighed on an analytical balance, and males were marked with red paint on the right elytron. Only adults weighing between 10–15 mg on the day of eclosion were used in the study. Mating of the weevils was facilitated by a 5-d conditioning period under the same environmental conditions used for rearing adults. During this period, mixed-sex groups of 20 weevils (10 males and 10 females) were held in 15-cm diameter petri dishes. Each dish was ventilated by a 4-cm diameter circular screened hole in the lid. Each dish contained a cotton wick saturated with water and was provisioned daily with five uninfested, greenhouse-grown squares (7–10 mm diameter at the widest part of the flower bud) with intact bracteoles. We assumed all females were mated by the end of the conditioning period.

Design of Experiments. Sixty 6-d-old female boll weevils were randomly selected from the conditioned population to provide estimates of feeding and oviposition activities and fecundity. The experimental treatments consisted of discrete levels of square availability. Twenty, 12, 10, 10, and 8 females were assigned to respective square availability treatments of 1, 5, 10, 15, and 20 squares per female. Each female was held individually in a plastic petri dish (15 by 2.5 cm) with a lid vented as previously described. The designated number of fresh uninfested greenhouse-grown squares (7–10 mm diameter) with intact bracteoles were provided to each female daily. Corresponding treatments with the same sample sizes were established for male weevils so the puncturing rates of the sexes could be compared. All weevils were held in an environmental chamber under the same environmental conditions used for rearing adults.

Squares were removed daily for the duration of each weevil's life, and punctures were counted under a

dissecting microscope. An oviposition puncture was distinguished from a feeding puncture by the presence of either a waxy substance sealing or encircling the opening of the punctures, a frass plug in the puncture, or the presence of both a frass plug and the waxy substance. Punctures lacking both characteristics were categorized as feeding punctures. Feeding punctures also tended to be somewhat larger in diameter than oviposition punctures.

The total number of punctures in each square (feeding + oviposition) was used as a measure of boll weevil puncturing activity according to the method of Everett and Earle (1964). Everett and Ray (1962) reported that the number of sealed punctures is a reliable estimate of oviposition. However, Cushman (1911) observed that many punctures containing eggs were not sealed with a frass plug. In addition, mated weevils occasionally deposit eggs on the external surfaces of the square (Mayer and Brazzel 1963). Recognizing these potential limitations, we used the number of oviposition (sealed) punctures as a relative measure of egg production, because most reports of boll weevil oviposition are based on such counts, and dissection of eggs from the squares would have prevented subsequent estimation of fecundity and survival.

Two daily cohorts, one of five and one of seven randomly selected squares with sealed punctures, were removed from each treatment and held in separate 15 by 1.5-cm petri dishes with ventilated tops under the same environmental conditions as the adults. The extent of egg hatch was estimated 2 d after oviposition by dissecting the cohort of five infested squares from each treatment for each of 35 d (35 total cohorts/treatment) and counting the number of larvae. Adult eclosion rate and sex ratio of emerged adults were determined for each treatment from the cohort of seven squares (40 total cohorts/treatment). Time for development from egg to adult was recorded for 10 individuals from each treatment. For the duration of each male's life, the squares were removed daily, and feeding punctures were counted under a dissecting microscope.

Statistical Analyses. The influence of square availability levels on adult longevity, life-time fecundity of females, numbers of feeding and oviposition punctures by females and males, and total development time of progeny (egg to adult) were examined with one-way analyses of variance (ANOVA) using PROC GLM (SAS Institute 1998). Because new cotton squares were provided daily for the entire life of each adult female and because longevity varied among individual females, statistical analyses were performed on daily observations of oviposition activity. The numbers of sealed punctures per square per day for each weevil were subjected to a repeated measures analysis, with time and the daily number of squares exposed as factors, using PROC MIXED of SAS (Littell et al. 1997). The number of oviposition punctures were $\log(x + 1)$ -transformed, and proportion data were arcsine-square root transformed before statistical analysis (Sokal and Rohlf 1981), but results are presented as

nontransformed means. Where significant F values were obtained, means were separated using Tukey's studentized range test ($\alpha = 0.05$; Wilkinson et al. 1992).

The homogeneity of boll weevil survival curves in the different treatments was tested by a likelihood ratio using the LIFETEST procedure of SAS (SAS Institute 1998). Subsequently, the LIFETEST procedure was used to perform pairwise comparisons of the survival curves.

For each of the five treatments, the sex ratio (male:female) of the total progeny of each female was first compared with a 1:1 ratio using a χ^2 test for goodness-of-fit. Then, an ANOVA was conducted to determine if sex ratio was affected by treatment.

The relationship between the number of squares punctured (y) by females and the number of squares offered (x) was described using the quadratic equation, $y = a + bx + cx^2$. The coefficients a , b , and c were calculated using the nonlinear function of SigmaPlot 5.0 (SPSS 2000).

An estimate of boll weevil population growth rate was obtained for each square availability treatment by calculating life table statistics (Southwood 1966). For each treatment, the jackknife program of Hulting et al. (1990) was used to calculate net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), the finite capacity of increase (λ , defined as the number of times a population multiplies itself per unit of time), mean generation time (T), doubling time (DT) of the population, and total progeny produced per female. The population growth index (GI) was calculated by dividing the percentage survival of immatures by development time (Sétamou et al. 1999).

Results

The number of lifetime punctures increased with square availability for both females ($F = 9.1$; $df = 4, 55$; $P < 0.01$) and males ($F = 14.4$; $df = 4, 55$; $P < 0.01$). Female feeding and oviposition punctures combined averaged 2.7-fold higher than the number of feeding punctures made by males across all treatments ($F = 16.8$; $df = 9, 110$; $P < 0.01$; Fig. 1).

The quadratic function, $y = 0.14 + 0.64x - 0.024x^2$, indicated a significant relationship between the mean number of squares punctured per day (y) and the number of squares offered per day (x) ($F = 41.7$; $df = 2, 58$; $P < 0.01$; $R^2 = 0.72$; Fig. 2). The mean number of squares punctured increased with availability to a peak of about 4 squares per day when offered 10–15 squares and decreased slightly when 20 squares were offered.

The number of squares provided per female did not significantly affect the proportion of progeny that were female or their development time (Table 1). However, square availability did affect estimated percent egg hatch ($F = 5.2$; $df = 4, 170$; $P < 0.01$) and subsequent survival to the adult stage ($F = 10.8$; $df = 4, 195$; $P < 0.01$). Both were significantly higher in the 10:1, 15:1, and 20:1 treatments than in the 1:1 and 5:1 treatments (Fig. 3).

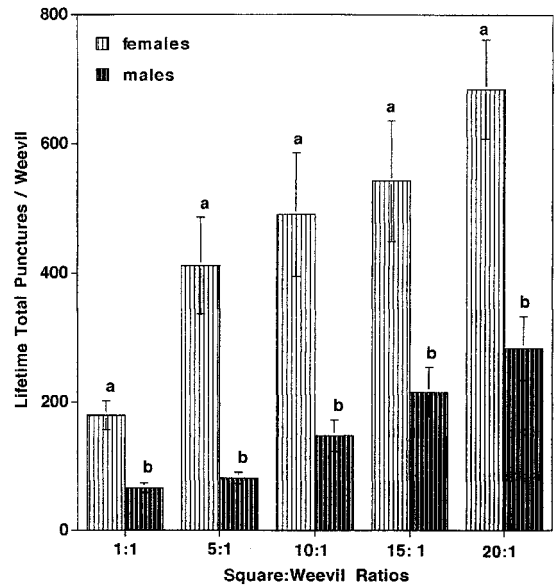


Fig. 1. Mean (\pm SE) lifetime punctures by boll weevil females and males provided different numbers of squares daily. Different letters indicate significant differences between sexes within a treatment (Tukey's honestly significant difference [HSD], $\alpha = 0.05$).

Fecundity (lifetime apparent oviposition) was about three-fold higher in the 10–20:1 treatments than in the 1:1 treatment (Table 1). Both time (day) ($F = 79.2$; $df = 1, 2,338$; $P < 0.01$) and number of squares available per boll weevil female ($F = 17.0$; $df = 4, 55$; $P < 0.01$) significantly affected the number of eggs oviposited (Fig. 4). In addition, the time by square availability interaction was significant ($F = 7.2$; $df = 4, 2,338$; $P < 0.01$), indicating that the temporal pattern of oviposition activity changed with changes in the number of squares available. When treatments were analyzed separately, the effects of time (day) significantly affected the number of eggs laid only for the

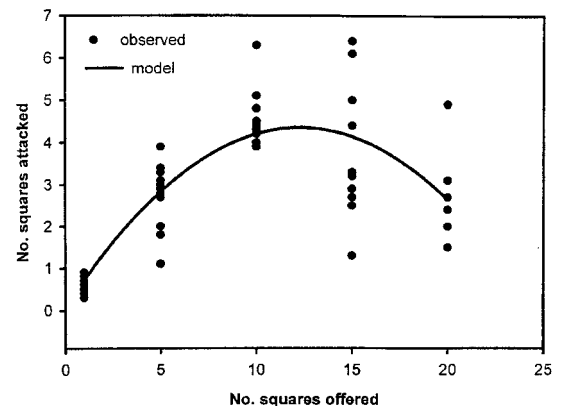


Fig. 2. A quadratic equation relating the mean number of squares attacked (punctured) per boll weevil female per day over their lifetime to the number of squares offered per day.

Table 1. Effects of the number of cotton squares provided daily per boll weevil female on sex ratio, development (egg to adult) times of progeny, lifetime fecundity, and longevity

Cotton squares per female per day	Percentage of female progeny ^a	Development time (d) ^b	Lifetime fecundity (sealed punctures)/female ^c	Longevity (d) ^d
1	40.1 ± 1.0a	22.7 ± 2.4a	83.2 ± 13.5b	37.1 ± 4.6b
5	43.4 ± 4.4a	21.2 ± 2.7a	187.6 ± 38.6ab	36.8 ± 5.1b
10	54.0 ± 3.4a	21.0 ± 3.8a	283.6 ± 44.7a	34.9 ± 4.8b
15	51.3 ± 2.8a	20.8 ± 2.8a	259.3 ± 39.2a	35.3 ± 6.6b
20	52.8 ± 2.3a	20.7 ± 4.4a	232.9 ± 38.0a	59.8 ± 3.1a

^a ANOVA: $F = 1.1$; $df = 4, 195$; $P = 0.374$. Means ($\pm SE$) did not differ significantly from 50% ($\chi^2 = 9.24$; $df = 4$; $P = 0.08$).

^b ANOVA: $F = 0.608$; $df = 4, 45$; $P = 0.659$.

^c ANOVA: $F = 7.8$; $df = 4, 55$; $P = 0.02$

^d ANOVA: $F = 2.9$; $df = 4, 55$; $P = 0.03$.

Means ($\pm SE$) within a column followed by the same letter are not significantly different (Tukey HSD, test).

10:1 ($F = 2.4$; $df = 58, 291$; $P < 0.01$; Fig. 4C) and 15:1 ($F = 2.3$; $df = 57, 334$; $P < 0.05$; Fig. 4D) treatments. In the 10:1 treatment, mean oviposition increased dramatically by the third day after eclosion, peaked near 15 sealed punctures per day at ≈ 10 d, and gradually declined thereafter (Fig. 4C). In contrast, when females were provided only one square per day, mean oviposition punctures plateaued by the second day of oviposition at ≈ 2.5 eggs per day, with slight increases occurring only at ≈ 6 wk, near the end of life (Fig. 4A).

The survivorship curves were significantly affected by the number of squares offered ($\chi^2 = 10.3$; $df = 4$; $P = 0.04$; Fig. 5). Longevity was significantly higher in the 20:1 treatment than in other treatments, which were similar (Table 1).

When boll weevil females were provided with 10, 15, or 20 cotton squares per day, the population growth indices (GI) were about two-fold higher than when weevils were provided only one or five squares (Fig. 6). A significant treatment effect on GI was indicated by the log-normal equation:

$$y = y_o + a \times e^{-0.5[\ln(x/x_o)/b]^2}$$

where $a = 1.6$, $b = 0.6$, $x_o = 12.6$, and $y_o = 0.8$.

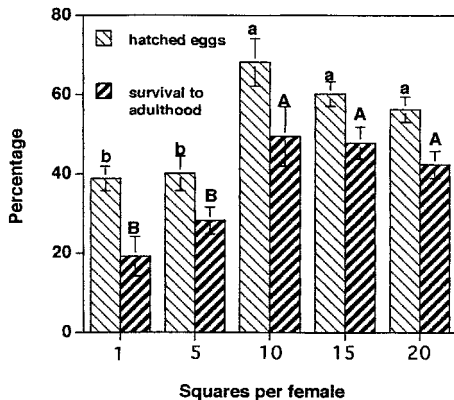


Fig. 3. Mean ($\pm SE$) percentage of eggs that hatched, and survival to adulthood, in relation to the number of squares provided per boll weevil female. Means with the same lowercase or uppercase letters, respectively, across treatments are not significantly different (Tukey's HSD, $\alpha = 0.05$).

The values of life table statistics calculated for boll weevil females varied with the ratio of squares to females (Table 2). The populations of boll weevils maintained at square:weevil ratios of 10:1, 15:1, or 20:1 were predicted to grow at significantly higher mean constant exponential rates (r_m) than those maintained on squares at ratios of 5:1 or 1:1. When the numbers of cotton squares were increased from 1 to 10, 15, or 20 per female, the total number of progeny produced per female increased 3.2- to 4.8-fold (Table 2). Life table calculations indicated that boll weevil populations maintained at a square:weevil ratio of 10:1 or above will increase >60 -fold each generation (R_0), a rate significantly higher than that exhibited under 5:1 or 1:1 square:female regimens.

Discussion

Boll weevil females produced 2.7 times more punctures than males. Hunter and Pierce (1912) reported that damage inflicted by female boll weevils is >5 times that of males, and Lloyd et al. (1961) also found that females damaged fruit at significantly higher rates than males. These results generally agree with our observations, but direct comparisons are not possible because of differing experimental conditions.

The quadratic function indicated that daily square availability of >15 squares per weevil resulted in a decrease in the total number of squares punctured. This apparent inconsistency suggests the observed reduction in the number of squares punctured at the highest level of square availability may have been artifactual or a consequence of the small sample size for that feeding treatment.

When resources are in short supply, competition between individuals within a population may reduce reproductive rate and survival (Varley et al. 1974). Our results suggest that boll weevil populations may be regulated in part by a density-dependent mechanism based on the availability of squares of suitable size and condition for oviposition. Estimates of the intrinsic rate of increase (r_m) and of the population growth index (GI) indicate that availability of oviposition sites become progressively more limiting as the ratio of squares to females decreases below 10:1. The manifestation of this limitation is three-fold. First, fe-

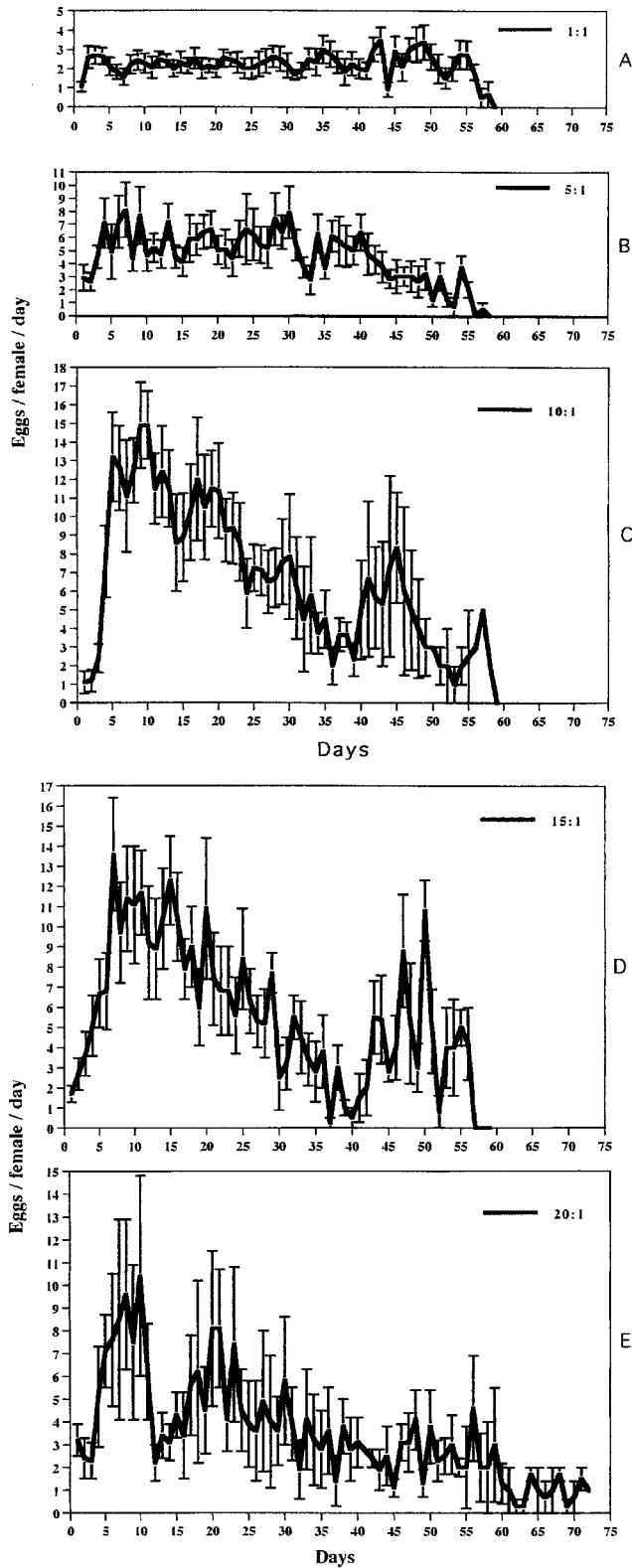


Fig. 4. Lifetime profiles of daily mean (\pm SE) oviposition activity of boll weevils in response to different levels of daily square availability (no. squares:female): (A) 1:1; (B) 5:1; (C) 10:1; (D) 15:1; and (E) 20:1.

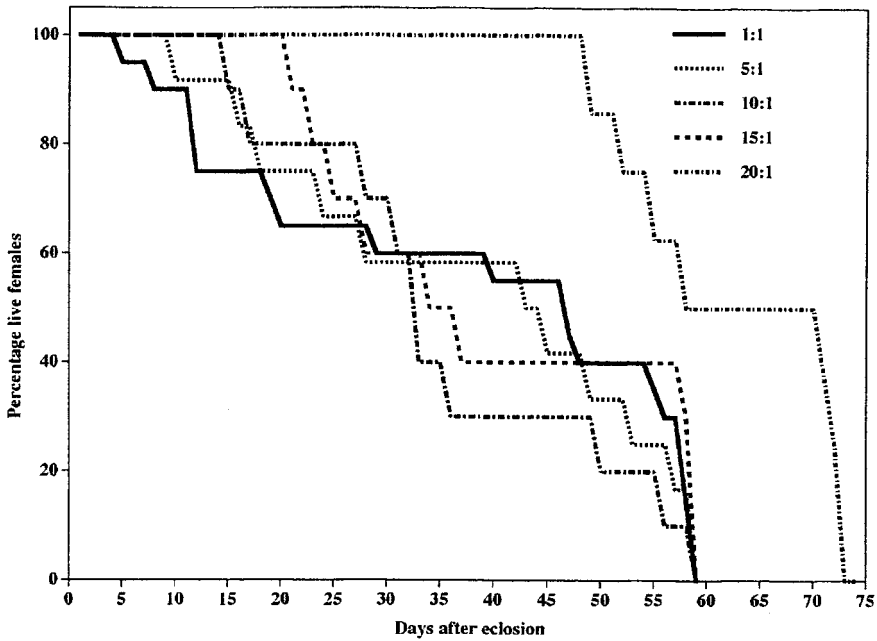


Fig. 5. Survivorship profiles of boll weevil females in response to different levels of daily square availability (1:1, 5:1, 10:1, 15:1, or 20:1, squares:female).

males laid fewer eggs per lifetime when provided with five or fewer squares per day. Although the percentage of squares infested with boll weevil larvae was ≈ 2.0 -fold greater in the 1:1 treatment than in the 10:1 treatment, there were fewer total punctures in the 1:1 and 5:1 treatments than in the 10:1 treatment. This suggests a reduction in oviposition and feeding behavior associated with an increase in square damage. Lifetime profiles of daily oviposition activity among females

with abundant or limited square availability (Fig. 4) reveal the consequences of an inadequate number of oviposition sites. Average longevity was the same in either case, and although females in the 1:1 treatment may have slightly increased their oviposition activity late in life, the number of oviposition punctures produced remained limited. Thus, our data suggest that heavily damaged squares negatively influence both oviposition and feeding behavior, either directly through negative cues associated with square damage or indirectly through the loss of positive cues associated with acceptable oviposition or feeding sites.

Second, the percentage of oviposited eggs that hatched, indicated by the presence of larvae, was lowest in the 5:1 and 1:1 treatments. It is possible that the higher number of punctures in these treatments increased the likelihood of direct damage to eggs already oviposited or negatively altered the microenvironment of oviposited eggs, perhaps through faster desiccation or decay of a heavily damaged square.

Finally, the percentage of larvae that survived to adulthood was lowest in the 5:1 and 1:1 treatments. Again, it is likely that deterioration of the heavily damaged squares contributed to low survival rates. Cannibalism or intraspecific competition among multiple larvae in a square may also have limited survival.

In summary, our data indicate that the daily number of undamaged squares to which boll weevil females have access affects the number of sealed punctures (and presumably the number of eggs laid), the number of feeding punctures, survival of progeny to adulthood, and the ultimate number of adult progeny produced per lifetime. The threshold at which squares

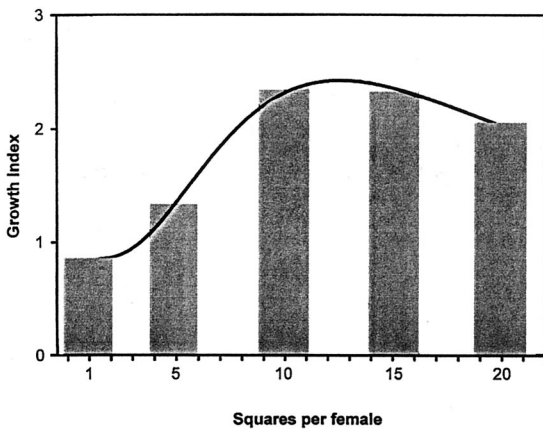


Fig. 6. Population growth indices of boll weevil females in relation to the number of squares offered. Growth index (GI) = percentage immature survival to adulthood divided by immature development time (d). The relationship between the GI and the number of squares provided was estimated with a log-normal equation ($F = 223.4$; $df = 3, 4$; $P = 0.05$).

Table 2. Life table statistics of boll weevil females as affected by the number of cotton squares provided daily per female (Values in parentheses are 95% confidence intervals)

Cotton squares per female	R_0	r_m	λ	T	DT	Total progeny
1	21.5 ± 3.5 (14.6–28.4)	0.241 ± 0.018 (0.201–0.289)	1.27	12.8	2.89	40.6 ± 6.6 (27.7–53.5)
5	32.6 ± 6.7 (19.5–45.7)	0.298 ± 0.021 (0.258–0.338)	1.35	11.7	2.34	75.4 ± 15.5 (45.0–105.8)
10	102.3 ± 16.1 (70.7–133.9)	0.446 ± 0.026 (0.396–0.496)	1.56	10.4	1.56	193.4 ± 30.5 (133.6–253.2)
15	80.0 ± 12.1 (56.3–103.7)	0.389 ± 0.026 (0.339–0.439)	1.47	11.3	1.76	156.1 ± 23.6 (109.7–202.4)
20	68.8 ± 11.3 (47.7–90.9)	0.395 ± 0.019 (0.355–0.435)	1.48	10.8	1.76	130.2 ± 21.4 (88.3–172.1)

R_0 , net reproductive rate; r_m , intrinsic rate of increase; λ , finite rate of increase; T , mean period over which progeny are produced (d); DT , doubling time of the population (d).

Total progeny production was calculated using the jackknife program of Hulting et al. (1990).

become limiting for these parameters seems to lie between 5 and 10 squares per female per day. The life table statistics generated from these data will help improve our capacity to predict square loss and changes in boll weevil populations in the field, given a starting density of suitable squares for oviposition and a corresponding starting population density of weevils.

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References Cited

- Bottrell, D. G. 1976. The boll weevil as a key pest, pp. 5–8. *In* Boll Weevil Suppression, Management, and Elimination Technology, Proceedings of a Conference, Memphis, TN. ARS-S-71. USDA, Washington, DC.
- Cole, C. L., and P. L. Adkisson. 1982. Effects of constant and variable temperature regimens on the survival and rate of increase of the boll weevil. *Southwest. Entomol.* 7: 50–55.
- Cushman, R. A. 1911. Studies on the biology of the boll weevil in the Mississippi delta region of Louisiana. *J. Econ. Entomol.* 4: 432–448.
- Everett, T. R., and J. O. Ray. 1962. The utility of sealed punctures for studying fecundity and egg laying by the boll weevil. *J. Econ. Entomol.* 55: 634–637.
- Everett, T. R., and N. W. Earle. 1964. Boll weevil oviposition responses in cotton squares and various other substrates. *J. Econ. Entomol.* 57: 651–656.
- Hulting, F. L., B. Orr, and J. J. Obrycki. 1990. A computer program for calculation and statistical comparison of intrinsic rates of increase and associated life table parameters. *Fla. Entomol.* 73: 601–612.
- Hunter, W. D., and W. D. Pierce. 1912. The Mexican boll weevil: a summary of the investigations of this insect up to December 31, 1911. U.S. Sen. Doc. 305. U.S. Senate, Washington, DC.
- Isley, D. 1928. Oviposition of the boll weevil in relation to food. *J. Econ. Entomol.* 21: 152–155.
- Lambert, L., G. L. Lentz, and E. T. Cherry. 1979. Preoviposition periods and oviposition rates of insectary-reared boll weevils in West Tennessee. *Environ. Entomol.* 8: 1092–1094.
- Littell, R. C., G. A. Milliken, W. W. Stoup, and R. D. Wolfinger. 1997. SAS system for mixed models. SAS Institute, Cary, NC.
- Lloyd, E. P., J. L. McMeans, and M. E. Merkl. 1961. Preferred feeding and egg-laying sites of the boll weevil and the effect of weevil damage on the cotton plant. *J. Econ. Entomol.* 54: 979–984.
- Mayer, M. S., and J. R. Brazzel. 1963. The mating behavior of the boll weevil, *Anthonomus grandis*. *J. Econ. Entomol.* 56: 605–609.
- Roach, S. H. 1979. Boll weevils: reproductive potential, feeding, and longevity of overwintering adults, and some effects of photoperiod on fecundity. *J. Ga. Entomol. Soc.* 14: 346–350.
- Sappington, T. W., and D. W. Spurgeon. 2000. Preferred technique for adult sex determination of the boll weevil (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* 93: 610–615.
- SAS Institute. 1998. JAS/STAT user's guide, release 6.03. SAS Institute, Cary, NC.
- Sétamou, M., F. Schulthess, N. A. Bosque-Perez, H. M. Poehling, and C. C. Borgemeister. 1999. Bionomics of *Mussidia nigricornis* (Lepidoptera: Pyralidae) on three host plants. *Bull. Entomol. Res.* 89: 465–471.
- SPSS. 2000. Sigmaplot 2000 user's guide, SPSS Inc., Chicago, IL.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., San Francisco, CA.
- Southwood, T.R.E. 1966. Ecological methods: with particular reference to the study of insect populations. Kluwer, Dordrecht, The Netherlands.
- Spurgeon, D. W., and J. R. Raulston. 1997. Boll weevil reproductive development under selected feeding regimes, pp. 982–984. *In* P. Dugger and D. A. Richter (eds.), Proceedings, Beltwide Cotton Conference. National Cotton Council, Memphis, TN.
- Sterling, W. L., and P. L. Adkisson. 1978. Population dynamics of the boll weevil inhabiting the High and Rolling Plains of Texas. *Environ. Entomol.* 7: 439–444.
- Varley, G. C., G. R. Gradwell, and M. P. Hassel. 1974. Insect population ecology: an analytical approach. University of California Press, Los Angeles, CA.
- Wilkinson, L., M. A. Hill, and E. Vang. 1992. SYSTAT: statistics, version 5.2. Systat, Inc., Evanston, IL.

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