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Influence of Different Cotton Fruit Sizes on Boll Weevil (Coleoptera: Curculionidae) Oviposition and Survival to Adulthood

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ABSTRACT Understanding the critical host plant factors that determine oviposition behavior and survival of boll weevil, *Anthonomus grandis grandis* Boheman, on cotton, *Gossypium hirsutum* L., is important for developing successful pest management strategies. However, published information is both conflicting and limited regarding how different cotton fruit sizes affect boll weevil oviposition choices and subsequent larval survival to adulthood. Consequently, we used a standard based on fruit size diameter to evaluate boll weevil feeding and oviposition punctures, and survival to adulthood on 10 different cotton fruit sizes: squares of diameter 1.5–2.0 (pinhead), 3.0–3.5 (matchhead), 5–6, 7–8, or 9–10 mm; candle; and bolls of diameter 10–15, 15–20, 20–30, or >30 mm. Oviposition and feeding punctures were significantly affected by cotton fruit size. Females did not oviposit in pinhead squares. The fewest eggs were oviposited in boll sizes >30 mm. The highest number of eggs was recorded in square sizes of 5–6 and 7–8 mm. Boll weevil survival to adulthood was highest on square sizes of 7–8 or 9–10 mm (58.6–59.7%). No survival occurred in matchhead squares or bolls >30 mm. Duration of development was longest on boll sizes of 15–20 and 20–30 mm (18.2–18.8 d). The growth index (percentage immature survival divided by immature developmental time) of female boll weevils was 2.8-fold higher in 7–8- or 9–10-mm diameter squares than in 20–30-mm diameter bolls. This study will improve our capacity to develop methods to predict fruit losses and changes in boll weevil populations in the field, given a starting density of fruit suitable for oviposition, and a corresponding initial population density of weevils.

KEY WORDS *Anthonomus grandis grandis*, boll weevil, cotton fruit sizes, feeding punctures, oviposition punctures

IDENTIFYING AND UNDERSTANDING THE factors that affect the oviposition behavior and survival of boll weevil, *Anthonomus grandis grandis* Boheman, in cotton, *Gossypium hirsutum* L., is important in designing and implementing successful control strategies. Oviposition behavior may influence population dynamics through variation in spatial and temporal placement of eggs within the host environment. Boll weevils prefer squares to bolls for food and oviposition sites (Hunter 1912, Howard 1921, Lloyd et al. 1961, Everett and Ray 1964, Jones et al. 1975, McKibben et al. 1982). However, not all developmental stages of cotton squares or bolls are preferred equally by ovipositing females, nor is it likely that all stages are equally suitable for development of weevil larvae. Fenton and Dunnam (1929) observed that egg deposition was most frequent in squares from 6 d old to 3 d before bloom, after which feeding punctures were more numerous. Cate et al. (1979) reported that ovipositing females avoided squares <7 mm in diameter, whereas McGovern et al. (1987) found that squares >8 mm were less preferred than smaller squares for oviposition. Wagner et al. (1996), in contrast, indicated no differences in oviposition preference for squares 3–9 mm in diameter. Thus, published information is both conflicting and limited regarding the oviposition behavior and survival to adulthood of boll weevils among different cotton fruit sizes. Our investigation used a standard based on fruit size diameter and our objectives were to evaluate laboratory feeding and oviposition activity of adult females, as well as developmental time, survival to adulthood, and sex ratio of offspring relative to different cotton fruit sizes.

Materials and Methods

Boll Weevil Culture and Cotton Squares. To help avoid potentially confounding effects of developmental history on our study, we reared all experimental

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Table 1. Mean (±SEM) punctures in different cotton fruit sizes by boll weevil females over the first 10 d of oviposition activity

Fruit size	Punctures per female per day			
	Feeding	Sealed	Total	Puncture ratio: sealed/total
Pinhead	2.2 ± 0.1d	0d	2.2 ± 0.1d	0d
Matchhead	2.8 ± 0.2d	2.8 ± 0.3c	5.6 ± 0.4c	0.473 ± 0.04b
Squares, diam. mm				
5–6	3.7 ± 0.3cd	7.3 ± 0.6a	11.0 ± 0.7b	0.648 ± 0.03a
7–8	3.5 ± 0.2cd	8.1 ± 0.6a	11.6 ± 0.6b	0.673 ± 0.04a
9–10	13.4 ± 1.0a	5.0 ± 0.6b	18.4 ± 1.4a	0.258 ± 0.02c
Candles	10.6 ± 0.9b	1.4 ± 0.2cd	12.0 ± 1.1b	0.103 ± 0.01d
Bolls, diam. mm				
10–15	5.1 ± 0.4c	2.7 ± 0.3c	7.8 ± 0.5c	0.335 ± 0.03bc
15–20	3.1 ± 0.2cd	2.9 ± 0.5c	6.0 ± 0.5c	0.430 ± 0.04b
20–30	3.6 ± 0.3cd	1.1 ± 0.2cd	4.7 ± 0.4cd	0.202 ± 0.04c
>30	1.8 ± 0.3d	0.07 ± 0.03d	1.9 ± 0.3d	0.032 ± 0.01d

Means within a column followed by the same letter are not significantly different (Tukey honestly significant difference, $P < 0.05$).

insects in the laboratory. Adult boll weevils were reared from larval-infested squares collected in the Lower Rio Grande Valley of Texas during summer 2001 and were provided with fresh, excised squares (7–10 mm in diameter) for feeding and oviposition. Infested squares were held in screen cages (20 by 20 by 20 cm) in an environmental chamber at 27 ± 1°C, 65% RH, and a photoperiod of 13:11 (L:D) h. After the completion of larval development, the pupae were harvested and placed in petri dishes (9 cm in diameter) containing a thin 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 (Painters Medium, Hunt Corp., Statesville, NC) on the right elytron. Only adults weighing between 10 and 15 mg on the day of eclosion were used in the study. Mating of the weevils was facilitated by a 5-d conditioning period by using the same environmental conditions that were used for rearing adults. During this period, 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 provided daily with uninfested, greenhouse-grown cotton squares (7–10 mm in diameter at the widest part of the flower bud) with intact bracts. We assumed all females were mated by the end of the conditioning period.

Experimental Design. Sequential plantings of cotton (DPL 451RR) were made in a greenhouse to ensure that the required quantity of square and boll sizes were available for simultaneous conduct of all experimental treatments. Females were assigned to one of 10 cotton fruit diameter sizes (treatments): 1.5–2.0-mm pinhead squares; 3.0–3.5-mm matchhead squares; 5–6-, 7–8-, and 9–10-mm squares; 1-d pre-

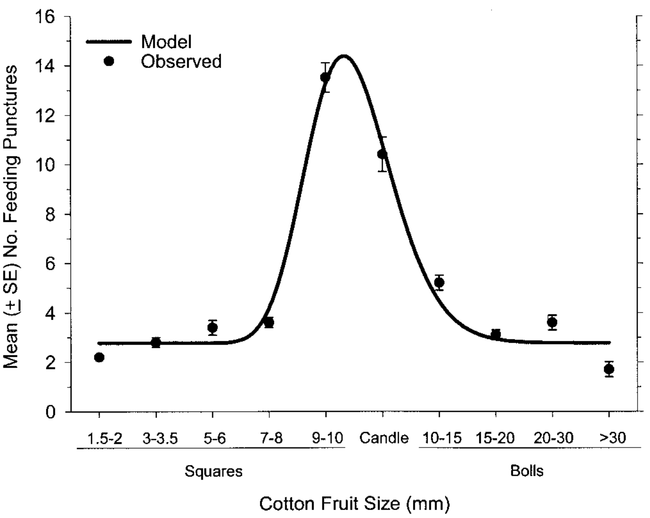

Fig. 1. Observed mean number of feeding punctures per boll weevil female per day in different cotton fruit sizes, and the peak function model fit to the data (see text for model parameters). The following cotton fruit diameter sizes are shown on the x-axis: 1.5–2-mm pinhead squares; 3–3.5-mm matchhead squares; 5–6-, 7–8-, and 9–10-mm squares; candles (i.e., 1-d prebloom squares); and 10–15-, 15–20-, 20–30-, and >30-mm bolls.

Table 2. Parameters of the peak functions describing the relationship between cotton fruit sizes and the number of sealed punctures caused by boll weevil (see Fig. 2)

Parameter	Estimate	SE	t value	P value
A. Group of cotton square sizes (R^2 = 0.989)				
a	8.81	0.39	22.67	<0.001
b	1.16	0.06	19.47	<0.001
x_o	3.72	0.06	63.33	<0.001
B. Group of cotton boll sizes (R^2 = 0.992)				
a	3.26	0.22	15.03	0.004
b	1.04	0.08	12.48	0.006
x_o	7.52	0.08	93.93	<0.001

bloom candle squares; and 10–15-, 15–20-, 20–30-, and >30-mm bolls. There were 20 replications (females) per treatment. Each female was isolated in a 15-cm-diameter ventilated petri dish (boll sizes of 20–30 mm and >30 mm required the use of a screen cage [20 by 20 by 20 cm] for isolation of each female assigned to these two treatments) and placed in an environmental chamber at 27 ± 1°C, 65% RH, and a photoperiod of 13:11 (L:D) h. Each female was provided with five uninfested fruits of the appropriate size, which were replaced daily for the first 10 d after onset of oviposition, after which the experiment was terminated.

Experimental Indices and Their Assessment. Fruits were removed daily and both feeding (open) and oviposition (sealed) punctures were counted under a dissecting microscope. The total number of punctures (feeding and oviposition) in each fruiting structure was used as a measure of boll weevil puncturing activity according to the method of Everett and Earle (1964). The number of sealed punctures is a relative estimate of the number of eggs oviposited (Everett and Ray 1962). An egg-puncture ratio (ratio of sealed to total punctures) was used to characterize oviposition activity (Everett and Earle 1964). Everett and Ray (1962) indicated oviposition could be adequately estimated by counts of sealed punctures rather than counts of actual eggs. Our preliminary laboratory studies indicated a high correlation between egg punctures and actual eggs (unpublished data). However, in other studies some unsealed punctures contained eggs (Cushman 1911), and eggs were occasionally deposited on the square surface (Coad 1915, Mayer and Brazzel 1963, Palumbo et al. 1990). Nevertheless, we deemed oviposition punctures the best option for measuring egg production, because the alternative, dissection of eggs from the squares, would have precluded subsequent survival estimates.

Apparently infested fruit (squares or bolls with sealed punctures) were placed in an environmental chamber (27 ± 1°C, 65% RH, and a photoperiod of 13:11 [L:D] h) to inhibit fruit desiccation and optimize development of weevil immatures to the adult stage. Data recorded included rate of successful development to adulthood from apparently infested fruit, developmental time, and percentage of female progeny. A growth index (GI) was calculated by dividing the percentage immature survival by developmental time (Sétamou et al. 1999). The GI provides an indication of the relative impact of the experimental treatments on the growth potential of a population. For each treatment, the female progeny produced per female was calculated by multiplying the sealed punctures per female per day, by the proportion of successful development, and the proportion of female progeny.

Statistical Analyses. We used one-way analysis of variance (ANOVA) tests to examine differences among the 10 treatments in the following weevil response variables: the daily number of feeding, sealed, and total punctures per female; the proportion of sealed punctures to total punctures per female per day; and developmental time, successful development to adulthood, and proportion female progeny. Whenever significant F values were obtained, means were separated using Tukey's studentized range test (Wilkinson et al. 1992). Percentage data were arcsine-square root transformed before statistical analysis (Sokal and Rohlf 1981), but results are presented as nontransformed means.

The relationships between cotton fruit size (x) and number of feeding punctures, sealed punctures, and ratio of sealed to total punctures (y) were described using the peak function. The relationship between cotton fruit sizes and the number of feeding punctures

Table 3. Parameters of the peak functions describing the relationship between cotton fruit sizes and the ratio of sealed to total punctures caused by boll weevil (see Fig. 3)

Parameter	Estimate	SE	t value	P value
A. Group of cotton square sizes (R^2 = 0.992)				
a	0.73	0.06	11.91	0.001
b	1.19	0.12	10.24	0.002
x_o	3.93	0.11	29.82	<0.001
B. Group of cotton boll sizes (R^2 = 0.990)				
a	0.43	0.03	15.44	0.004
b	1.05	0.08	13.06	0.006
x_o	7.71	0.08	98.48	<0.001

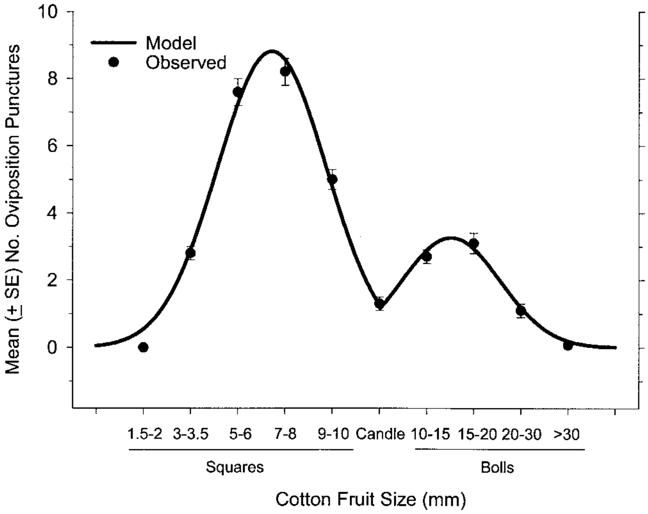

Fig. 2. Observed mean number of sealed (oviposition) punctures per boll weevil female per day in different cotton fruit sizes, and the peak function models fit to the data (see Table 2 for model parameters). The x-axis as described for Fig. 1.

was best described by one model with four parameters, $y = y_0 + a^*\exp[-0.5^*(x - x_0)/b)^2]$ (1). The effect of cotton fruit size on the number of sealed punctures, and on the ratio of sealed to total punctures was described by a segmented model combining two peak functions of three parameters each for the square and boll sizes (treatments), respectively, $y = a^*\exp[-0.5^*(x - x_0)/b)^2]$ (2). The relationships between cotton fruit size (x) and successful development rate and GI (y) were described using the log-normal function $y = a^*\exp[-0.5^*(\ln x/x_0)/b)^2]$ (3). All parameters (a, b, x_0, and y_0) of the different functions were calculated using SigmaPlot 5.0 (SPSS 2000).

Results

The number of feeding and sealed punctures was significantly affected by cotton fruit size ($F_{9, 190} = 43.2$; $P < 0.001$, and $F_{9, 190} = 64.3$; $P < 0.001$, respectively) (Table 1). Females did not oviposit in pinhead squares. The fewest sealed punctures were in candles and bolls 20–30 or >30 mm in diameter. The highest number of sealed punctures was recorded for treatments containing squares 5–6 and 7–8 mm in diameter. The total number of punctures per day was significantly greater for squares 9–10 mm in diameter than for any other fruit size. The ratio of sealed to total punctures, characterizing oviposition activity, was af-

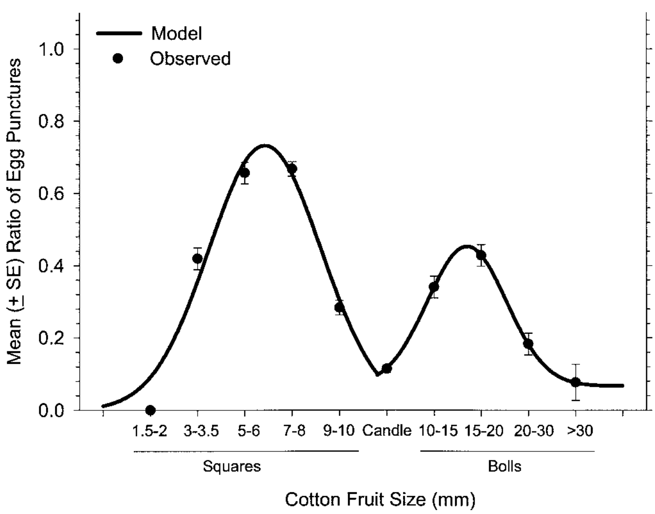

Fig. 3. Observed mean ratio of sealed to total punctures per boll weevil female per day in different cotton fruit sizes, and the peak function models fit to the data (see Table 3 for model parameters). The x-axis as described for Fig. 1.

Table 4. Mean (±SEM) number and percentage of cotton fruit punctured per day by boll weevil females among different fruit sizes

Fruit size	Fruit punctured	% Fruit punctured
Pinhead	1.9 ± 0.2	37.8 ± 3.1c
Matchhead	3.2 ± 0.2	64.8 ± 3.8b
Squares, diam. mm		
5–6	4.0 ± 0.3	80.9 ± 7.0ab
7–8	4.6 ± 0.1	91.6 ± 1.6a
9–10	4.4 ± 0.1	88.4 ± 2.0a
Candles	3.2 ± 0.3	64.9 ± 6.5b
Bolls, diam. mm		
10–15	3.3 ± 0.2	65.6 ± 3.9b
15–20	3.2 ± 0.3	63.1 ± 5.7b
20–30	2.1 ± 0.3	42.6 ± 6.1c
>30	1.2 ± 0.2	23.1 ± 3.6c

Means within a column followed by the same letter are not significantly different (Tukey honestly significant difference, $P < 0.05$); n = 5 cohorts of total 500 squares/treatment.

Table 5. Mean (±SEM) developmental time to adulthood, and percentage of female progeny of boll weevils on different cotton fruit sizes

Fruit size	Development time, d (n^a)	Female progeny, % ($n_1{}^b$)	Mean daily production of female offspring per female
Squares, diam. mm			
5–6	15.9 ± 1.7b	46.5 ± 1.4a (231)	1.2
7–8	16.4 ± 1.4b	54.3 ± 1.8a (441)	2.6
9–10	16.2 ± 0.8b	52.1 ± 0.5a (264)	1.5
Candles	16.6 ± 1.3b	47.8 ± 8.6a (52)	0.2
Bolls, diam. mm			
10–15	15.9 ± 1.4b	49.2 ± 2.0a (77)	0.4
15–20	18.2 ± 1.5a	50.6 ± 1.8a (78)	0.4
20–30	18.8 ± 1.4a	43.9 ± 2.4a (35)	0.1

Means within a column followed by the same letter are not significantly different (Tukey honestly significant difference, $P < 0.05$).
[a] n = 10 adults per treatment.
[b] n_1 = total adults of five cohorts per treatment.

fected by fruit size ($F_{9,\ 190} = 54.6$; $P = 0.001$). It did not differ significantly among squares of 5–6 mm ($P = 0.656$) and 7–8 mm ($P = 0.667$) in diameter, but these were significantly higher than the other treatments (Table 1).

The peak equations indicated a significant relationship between cotton fruit size (x) and feeding punctures (y), with $y = 2.8 + 11.6*\exp\{-0.5*[(x - 5.3)/0.1]^2\}$ ($F_{3,\ 9} = 71.4$; $P < 0.001$; $R^2 = 0.97$) (Fig. 1). Similarly, significant effects of cotton fruit size (x) on sealed punctures (y), and on the ratio of sealed to total punctures were recorded (Tables 2 and 3; Figs. 2 and 3), with higher coefficients a and b being obtained for the squares compared with that obtained for the bolls.

The percentage of fruit punctured per day was significantly affected by fruit size ($F_{9,\ 40} = 24.9$; $P < 0.001$) (Table 4). Females were 1.7-fold more likely to puncture squares 5–6, 7–8, and 9–10 mm in diameter (~81–92% punctured fruit) than those of other sizes (~23–66%).

Successful development of boll weevils to adulthood varied significantly with cotton fruit size ($F_{9,\ 40} = 80.7$; $P < 0.001$) (Fig. 4). No adults were produced from pinhead squares, matchhead squares, or bolls >30 mm in diameter. The log-normal equations indicated a significant relationship between successful development of boll weevils to adulthood (y) and cotton fruit size (x), $y = 58.3*\exp\{-0.5*[(\ln x/4.6)/0.4]^2\}$ ($F_{2,\ 9} = 32.7$; $P < 0.001$; $R^2 = 0.90$).

Boll weevil females provided with 7–8-mm-diameter squares produced 54.3% female progeny, compared with 43.9% for those provided with 20–30-mm-diameter bolls (Table 5); however, this difference was not significant ($F_{6,\ 28} = 5.6$; $P = 0.192$). The mean daily

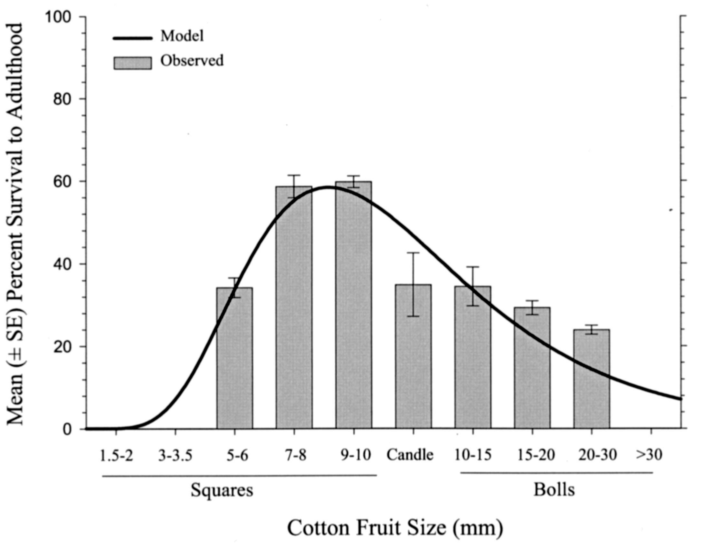

Fig. 4. Successful development of boll weevil to adulthood in different cotton fruit sizes, and the log-normal model fit to the data (see text for model parameters). The x-axis as described for Fig. 1.

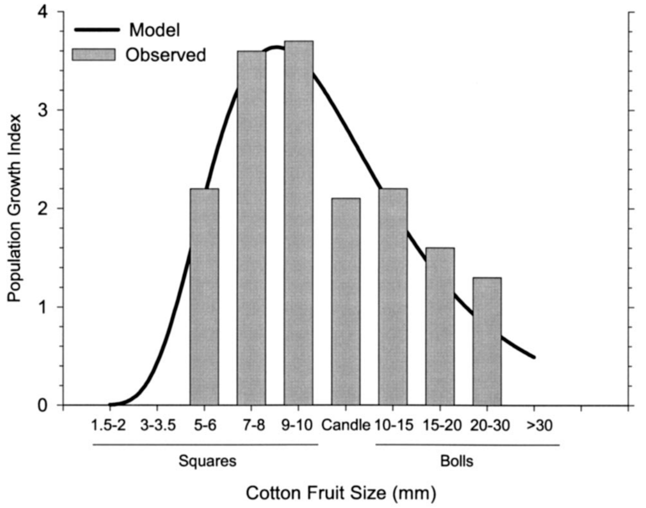

Fig. 5. Observed population growth indices for boll weevil females when provided with cotton fruit of different sizes. The x-axis as described for Fig. 1.

number of female progeny produced per female on 7–8-mm-diameter squares was 26-fold greater than those produced on 20–30-mm-diameter bolls (Table 5). Developmental time of boll weevil females was affected by fruit size ($F_{6, 63} = 7.3$; $P < 0.001$) and was significantly longer when they developed on bolls 15–20 or 20–30 mm in diameter than on squares larger than matchhead, candles, or small bolls (Table 5).

The population growth indices (GI) were 2.8-fold higher on fruit 7–8 and 9–10 mm in diameter than on bolls 20–30 mm in diameter (Fig. 5). A significant effect of fruit size on GI was indicated by the log-normal equation $y = 3.6*\exp\{-0.5*[(\ln x/4.5)/0.4]^2\}$ ($F_{2, 9} = 39.5$; $P < 0.001$; $R^2 = 0.92$).

Discussion

Many researchers have addressed various aspects of feeding and oviposition behavior of boll weevil on cotton; however, there is apparently no information about the effect of very young cotton fruit (pinhead and matchhead squares) on feeding and oviposition behavior of weevils. Also, data relating different cotton fruit sizes to important population parameters such as successful development to adulthood, population growth index, and female progeny produced per boll weevil are limited.

There are several reports about boll weevil feeding and oviposition preference for cotton fruit. Townsend (1895) observed that female weevils deposited eggs in squares and small bolls. Hunter (1912) and Howard (1921) showed that squares were the preferred place for feeding and oviposition. Hunter and Pierce (1912) reported that squares of intermediate size were preferred for oviposition, whereas Everett and Earle (1964) suggested that cotton squares weighing 300–350 mg were most attractive. Everett and Ray (1964) concluded that boll weevils prefer squares weighing an average 319 mg, which are ≈11–12 d old and ≈6 mm in diameter (Jones et al. 1975). Fenton and Dunnam (1929) stated that weevils most frequently deposited eggs in squares from 6 d old until 3 d before bloom. In squares ≈3 d from blooming, feeding punctures were more numerous. McGovern et al. (1987) observed that the size of squares influenced oviposition preference, with squares >8 mm being less preferred. No eggs were oviposited in squares measuring ≈9.5 mm. Isley (1928) reported that longevity and egg production were influenced greatly by the type of food consumed. Survival and egg production were greatest when weevils were fed squares, but egg production stopped when weevils were fed large bolls. The number of eggs deposited by weevils fed exclusively on squares was much greater than by those fed exclusively on bolls (Isley 1932). Tingle et al. (1971) observed that when only bolls are available for feeding or if there is a shortage of squares, boll weevils store body fat and the reproductive organs tend to atrophy. Bolls 1–3 d old had a 60% probability of being damaged, whereas bolls 11–13 d old had about a 20% probability of being damaged (Walker et al. 1977).

These cited studies generally agree with our observations, but direct comparisons are difficult because of differing experimental conditions (field versus laboratory, choice versus no-choice) and categorization of fruit classes (measurements of fruit relative to weight, diameter size, or age in days). Our investigation used a standard based on fruit size diameter to determine the influence of different cotton fruit sizes on oviposition and survival to adulthood. The data in this article show that the numbers of oviposition (Fig. 2, sealed) and feeding punctures (Fig. 1) produced per female per day, as well as the puncture ratios (Fig. 3, sealed/total punctures) were significantly affected by cotton fruit size. The highest survival (Fig. 4), growth index (Fig. 5), and female progeny produced per boll weevil female (Table 5) were observed when the weevils developed on squares of 7–8- or 9–10-mm diameter.

We are interested in improving our ability to predict fruit losses and changes in boll weevil populations in the field. Such predictions require, at a minimum, knowing the density of fruit suitable for oviposition and development, the relative preference of boll weevil for different fruit sizes, and the corresponding starting population density of weevils. The results of this study provide qualitative meaning to fruit "suitability," which changes with fruit development and phenology. Quantification of behavioral choices of weevils among fruit of different sizes, both within a field and across fields at the landscape level, will be a difficult task because of the complexities involved, including the dynamics of fruit density and size profiles over time. However, the results would be of great value to our predictive efforts when combined with those presented here, and such experimentation is the next logical step.

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