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# Life History of Immature Maize Weevils (Coleoptera: Curculionidae) on Corn Stored at Constant Temperatures and Relative Humidities in the Laboratory

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**ABSTRACT** Life history of immature maize weevils, *Sitophilus zeamais* Motschulsky, was studied at 10–40°C and 43–76% RH. The optimal quantity of corn for minimizing density effects and the optimal observation frequency for minimizing disturbance effects were determined at 30°C and 75% RH. The quantity of corn (32–256 g) provided to five females ovipositing for 24 h did not affect duration of development, but the number of progeny produced increased asymptotically as the quantity of corn provided increased. Frequency of observation (from 1- to 14-d intervals) did not affect duration of development or number of progeny produced. Using moisture contents measured in the life history study, an equation was developed for predicting equilibrium moisture content of corn from temperature and relative humidity. Duration of immature development did not vary with sex, but did vary with test. This suggests that insect strain or chemical composition of the corn must be included as factors in a model predicting effects of environment on duration of immature development. Survival from egg to adult emergence was greatest at 25°C. Sex ratio of emerging adults did not differ from 1:1. The number of multiply-infested kernels was low at all environmental conditions, and survival from egg to adult emergence in these kernels averaged 18%. Maximum daily rate of fecundity, duration of development, and number of progeny produced were optimal at 30°C and 75% RH. An index of environmental suitability indicated that 30°C and 75% RH was the optimal environment for growth of maize weevil populations on corn. Implications of the results for managing maize weevil populations are discussed.

**KEY WORDS** life history, *Sitophilus zeamais*, *Zea mays*

THE MAIZE WEEVIL, *Sitophilus zeamais* Motschulsky, is a cosmopolitan pest of stored grain (Throne 1986). Despite the importance of this pest, quantitative data describing its life history over the range of environmental conditions at which it will develop are lacking. Such data can be used to define optimal storage conditions to reduce damage by the pest (Birch 1953) and to develop simulation models that can be used to optimize pest management strategies (Ruesink 1976).

There have been numerous reports on duration of development from egg to emergence of adult maize weevils (*S. zeamais* = large strain of *Calandra oryzae*; Birch 1944, Howe 1952, Satomi 1960, Chesnut & Douglas 1971, Hwang et al. 1983). However, these studies are all lacking in some manner. The ranges of temperatures and relative humidities at which a study was conducted usually were limited and did not reflect the environmental conditions at which grain is stored. The insect density usually was chosen for convenience; thus, the development times and number of progeny produced may be influenced by crowding. A measure of variance in development time generally was not reported. A measure of variance can be used to simulate variation in development time in population dynamics models (Wagner 1984). Only one of the previous studies examined development on corn, *Zea mays* L. (Chesnut & Douglas 1971). Life history of the maize weevil differs with grain type (Birch 1953).

This study was undertaken to determine duration of immature development of maize weevils on corn stored over the range of temperatures and relative humidities that would normally occur in storage. The intent was to optimize development conditions and to report data in a manner useful for developing a simulation model of maize weevil population dynamics. Effects of density and observation frequency on development were determined to optimize development conditions. Data describing the effects of tem-

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perature and relative humidity on maximum rate of fecundity, sex ratio, stage-specific survivorship, and survivorship in multiply-infested kernels (kernels that have more than one maize weevil developing in them) also are presented.

## Materials and Methods

**Density Optimization.** 'Pioneer 3320', a dent corn commonly grown in the southeastern United States, was used. The corn was from the 1987 crop, was commercially cleaned to remove large objects and small particles, and was sieved over a U.S. standard number 6 sieve (sieve openings 3.35 mm) before use. The corn was fumigated with phosphine shortly after purchase, stored at ≈5°C, and frozen at ≈−2°C for at least 2 wk before use to ensure disinfestation.

Weevils were from a culture maintained at 25 ± 1°C, 65–70% RH, and a photoperiod of 12:12 (L:D) h. The culture was founded with weevils collected from grain storage areas in southern South Carolina in 1985, and weevils from the field were added to the culture monthly. Voucher specimens were placed in the Florida State Collection of Arthropods (numbers JT1-JT6).

Lots of 32.00, 64.00, 128.00, and 256.00 ± 0.01 g of corn were placed in each of five cages (five replications of four lot sizes). Mean weight of 100-kernel lots was 32.42 g (SD = 1.03, $n$ = 21). Thus, the weighed lots of corn contained ≈100, 200, 400, and 800 kernels, respectively. Cages were constructed from clear acrylic tubes (Commercial Plastics, Atlanta, GA) and consisted of a lid and a base (dimensions of bases of 100-kernel cages: 38 mm i.d. by 38 mm high; 200-kernel cages: 50 mm i.d. by 45 mm high; and 400- and 800-kernel cages: 76 mm i.d. by 71 mm high). One end of each base and lid was covered with 64-$\mu$ mesh, nylon screen (Tetko, Briarcliff Manor, NY).

The cages of corn were placed on a perforated false floor in two covered plastic boxes (40 by 27.5 by 16 cm high; four lot sizes by three replications in one box and four lot sizes by two replications in the other box). The boxes each contained a saturated NaCl solution below the false floor to maintain 75% RH (Greenspan 1977). An additional cage containing a 300-g sample of corn was placed in each box and the moisture content of those 300-g samples was measured weekly with a moisture tester (Burrows DMC-700, Seedburo Equipment, Chicago, IL). The boxes were placed in an environmental chamber maintained at 30 ± 1°C and a photoperiod of 12:12 (L:D) h, and the corn was equilibrated to test conditions for 6 wk. These environmental conditions were chosen because they are nearly optimal for maize weevil oviposition and development (Hwang et al. 1983). Presumably, if density effects are minimized at optimal conditions, then they also will be minimized at suboptimal conditions.

After the 6-wk equilibration period, five females (2–3 wk old, second-laboratory generation) were placed in each cage. Sex was determined by snout characteristics (Tolpo & Morrison 1965) after immobilization of weevils by chilling. Females were sieved from the cages after 48 h with a U.S. standard number 6 sieve. Species and sex were confirmed based on examination of genitalia (Halstead 1962). Starting 3 wk after females were removed, emerging $F_1$ adult progeny were sieved from the corn every 3.5 d. $F_1$ progeny were considered to be those that emerged in <3.5 wk (time to first emergence) after more than one adult progeny were first observed in a cage.

The test was repeated two more times. Differences in test methods were that ovipositing females were 1–2 wk old, third laboratory-generation adults in the second test. A Motomco model 919 automatic grain moisture tester (Dickey-John, Auburn, IL) was used to measure moisture content in the second and third tests.

Treatment effects were analyzed using analysis of variance (SAS Institute 1987). Parameters for an asymptotic equation to describe the relationship between number of progeny produced and weight of corn provided were estimated by nonlinear regression (SAS Institute 1987).

**Sieving Frequency.** Lots of 224.00 ± 0.01 g of corn were placed in each of 25 cages (75 mm i.d. by 76 mm high). Ten cages of corn were placed in each of two plastic boxes and five cages of corn were placed in another box, all containing saturated NaCl solutions (five blocks of five treatment cages). Moisture content was monitored and environmental conditions were as in the previous experiment.

After the 6-wk equilibration period, five females (2–3 week old, second-laboratory generation) were placed in each cage for 48 h. Starting 3 wk after females were removed, emerging $F_1$ adult progeny were sieved from the corn every 1, 2, 3, 7, or 14 d. $F_1$ progeny were considered to be those that emerged <7 wk after the ovipositing females were removed. The test was repeated three more times. Treatment effects were analyzed using a general linear models procedure (SAS Institute 1987).

**Immature Development.** *Experimental Design.* Duration of development from egg to adult emergence was determined at seven temperatures (10, 15, 20, 25, 30, 35, and 40°C) over three saturated salt solutions ($K_2CO_3$, NaBr, and NaCl). Over the temperature range studied, these salt solutions maintain relative humidities of 43, 53–62, and 75–76%, respectively (Greenspan 1977).

Broken kernels left after cleaning were removed. Lots of 256.0 ± 0.1 g of corn were placed in each of 63 (21 environmental conditions by three replications) test cages (8 cm high by 8.4

cm i.d. at top of base; 64-$\mu$ mesh, nylon screen covering 6-cm hole in lid and base) (Model T15AC; TriState, Henderson, KY), lots of 300.0 ± 0.1 g of corn were placed in 21 cages to monitor moisture content, and lots of 128.0 ± 0.1 g of corn (≈400 kernels) were placed in 21 acrylic cages (75 mm i.d. by 74 mm high) for holding weevils before infestation of the test corn. Three test cages of corn, one moisture content sample, and one 400-kernel cage of corn were placed in each of 21 plastic boxes (seven temperatures by three relative humidities). The boxes were placed in environmental chambers maintained at appropriate temperatures and a photoperiod of 12:12 (L:D) h to equilibrate the corn to test conditions.

Five weeks later, 80 unsexed weevils (1–2 wk old, second-generation laboratory strain) were placed in each of the 400-kernel cages. These weevils were subjected to the test conditions for 1 wk to acclimate, after which 10 females were placed in each of the three test cages at each environmental condition. At some environmental conditions, 30 live females were not available after the 1-wk acclimation period because of death or uneven sex ratios. Thus, excess weevils from similar environmental conditions were substituted. Females were sieved from test cages after 24 h and species and sex were confirmed (Halstead 1962). I noted during dissection that eggs in the ovaries of weevils maintained at 35°C or higher were not well developed.

Two weeks after females were removed from the 400-kernel cages of corn, these lots of corn were sieved each week until adult progeny began to emerge. This indicated when to start sieving the test corn daily. (Test corn at 15°C was sieved weekly.) Thus, I was able to avoid exposing the test corn to ambient conditions until weevils were ready to emerge.

After emergence appeared complete, kernels in test cages were placed in a single layer on sheets of cellulose (previously exposed 13 by 18 cm radiographs) that were coated with double-stick tape. A sheet of corn kernels was placed on a sheet of film (Kodak Industrex M X-ray film in Ready Pack II foil packs, Eastman Kodak, Rochester, NY) placed 56 cm below an X-ray source (Model 43855A Faxitron, Hewlett-Packard, McMinnville, OR), and exposed for 4 min at 18 Kv and 3 mA. Negatives were examined under a stereomicroscope at a minimum of 12X magnification for the presence of any weevil stage. If the insect appeared to be dead (e.g., desiccated), the kernel was dissected to ensure life status and stage at death. If on the negatives the insect appeared to be alive, the kernel was returned to test conditions and X-rayed periodically to determine life status. The moisture content samples were X-rayed to determine numbers of weevils present in the corn before use in the test.

The test was repeated once more. Differences in methods were that environmental conditions were changed to 15, 17.5, 20, 25, 30, 32.5 (no $K_2CO_3$), and 35°C (no $K_2CO_3$); the corn was from the 1990 crop; weevils were second- and third-generation laboratory strains and were 1–4 wk old when placed in 400-kernel cages; 170 unsexed weevils were placed in each of the 400-kernel samples of corn; and 20 females were placed in test cages (except for 15 females at 25°C NaCl and 10 females at 30°C NaCl) to increase the number of progeny produced at nonoptimal conditions. Mean weight of 100-kernel lots of 1990 corn was 27.12 g (SD = 0.85, $n$ = 113).

*Moisture Content Analysis.* General equations for describing the effects of equilibrium temperature and relative humidity on moisture content of grain are useful in developing simulation models (e.g., predicting moisture content based on measured temperature and relative humidity) and for predicting storage conditions for grain. One such equation for corn is the Chung-Pfost equation (Pfost et al. 1976):

$$MC = a - [b * \log_e\{-1.987(T + c) * \log_e(RH)\}], \quad (1)$$

where $MC$ = % moisture content/100, $T$ = temperature (°C), $RH$ = % relative humidity/100, $a$ = 0.3387, $b$ = 0.05897, and $c$ = 30.21. The Chung-Pfost equation was used to calculate expected moisture contents for this study. In addition, values for $a$, $b$, and $c$ were calculated for the Chung-Pfost equation fit to observed moisture contents using nonlinear regression (SAS Institute 1987) and a new equation was developed using linear regression analysis (SAS Institute 1987) to fit an equation to the moisture content data from the current study.

*Duration of Development Analysis.* A general linear models procedure (SAS Institute 1987) was used to test for differences in duration of immature development among treatments. The data were analyzed as a multi-split-plot design with tests, temperatures, relative humidities, cages (nested within test, temperature, and relative humidity), and sexes as classes. Relative humidities used were means of those reported by Greenspan (1977) over the range of temperatures used in this study (NaCl: 75.2%; NaBr: 57.7%; and $K_2CO_3$: 43.2%). Either relative humidity or moisture content could be used as a classification factor because they are mathematically related (equation 1). Relative humidity was used as a classification factor because it is a calculated value (can be obtained from a table [Greenspan 1977]) and is not subject to measurement error. The data were transformed before analysis as:

$$\frac{\text{duration}^{0.21} - 1}{0.21} \quad (2)$$

to equalize variances (Box & Cox 1964).

TableCurve3D curve-fitting software (Jandel Scientific, San Rafael, CA) was used to fit many different types of equations to the data for duration of development (mean for each cage) versus temperature and relative humidity. The equations were fit to both duration of development and rate of development data (Kramer et al. 1991) and without weighting and with weighting by number of weevils emerged in a cage. Selection of an equation to describe the data was based on the magnitude and the pattern of residuals, lack of fit tests (Draper & Smith 1981), and whether the response surface had a shape that was reasonable for describing the data.

*Fecundity, Survival, Multiply-Infested Kernels, and Sex Ratio Analysis.* The number of eggs laid during the 24-h oviposition period divided by the number of females is indicative of maximum daily fecundity because density effects were minimized and females were at the age at which maximum daily fecundity is expected for weevils reared at 25°C (Segrove 1951). The number of eggs laid was determined by examination of the radiographs of the corn, and was calculated as the sum of the number of dead insects in each stage and the number of progeny emerged. This number was corrected for previous infestation of the corn by subtracting the product of the mean number of eggs laid in all moisture content samples (sum of dead insects and progeny emerged) and 256/300 (256 g of corn in treatment cages/300 g of corn in moisture content samples). If the corrected number of eggs laid in a cage was <0 or less than the number of progeny that emerged in that cage, then the number of eggs laid in that cage was set to the greater of 0 or the number of progeny that emerged in the cage, respectively.

A general linear models procedure (SAS Institute 1987) was used to determine whether there were differences among treatments in number of eggs laid per female during the 24-h oviposition period, in proportion survival of each weevil stage, in number of multiply-infested kernels, in number of weevils per multiply-infested kernel, and in proportion survival in multiply-infested kernels. Differences in sex ratios among treatments were tested by comparing the proportion females within cages after weighting the data by number of weevils emerged in a cage. The data were analyzed as a multi-split-plot design with tests, temperature, and relative humidity as classes. TableCurve3D was used to fit equations to maximum fecundity and proportion survival from egg to adult emergence data.

*Susceptibility Index.* A susceptibility index (Dobie 1974) was used to compare various temperature and relative humidity combinations for their relative suitability for maize weevil development. This index is calculated as $(\log_e y)/t$, where $y$ = number of progeny produced in a given environment and $t$ = duration of develop

**Table 1. Analysis of variance results**

| Source | df | $F$ | $P > F$ |
|---|---|---|---|
| Density optimization—Duration of development | | | |
| Test | 2, 54 | 5.99 | <0.01 |
| Quantity of corn | 3, 54 | 7.15 | <0.01 |
| Density optimization—Number of progeny | | | |
| Test | 2, 54 | 10.62 | <0.01 |
| Quantity of corn | 3, 54 | 9.95 | <0.01 |
| Sieving frequency—Duration of development | | | |
| Test | 3, 90 | 7.35 | <0.01 |
| Sieving frequency | 4, 90 | 0.30 | 0.87 |
| Sieving frequency—Number of progeny | | | |
| Test | 3, 90 | 83.99 | <0.01 |
| Sieving frequency | 4, 90 | 1.26 | 0.29 |
| Immature development—Duration of development—2 tests combined | | | |
| Test | 1, 3 | 0.15 | 0.73 |
| Temperature | 5, 3 | 48.07 | <0.01 |
| Relative humidity | 2, 2 | 166.62 | 0.01 |
| Test * temperature | 3, 1,058 | 16.97 | <0.01 |
| Immature development—Duration of development—Test 1 | | | |
| Sex | 1, 11 | 0.87 | 0.37 |
| Immature development—Duration of development—Test 2 | | | |
| Sex | 1, 19 | 0.86 | 0.36 |
| Fecundity | | | |
| Test | 1, 4 | 1.95 | 0.24 |
| Temperature | 8, 4 | 11.94 | 0.01 |
| Relative humidity | 2, 7 | 81.42 | <0.01 |
| Survival—Eggs | | | |
| Test | 1, 4 | 0.27 | 0.63 |
| Temperature | 8, 4 | 0.27 | 0.95 |
| Relative humidity | 2, 7 | 0.56 | 0.59 |
| Survival—Larvae | | | |
| Test | 1, 4 | 2.02 | 0.23 |
| Temperature | 8, 4 | 3.85 | 0.10 |
| Relative humidity | 2, 7 | 3.56 | 0.09 |
| Survival—Pupae | | | |
| Test | 1, 4 | 1.87 | 0.24 |
| Temperature | 8, 4 | 1.96 | 0.27 |
| Relative humdity | 2, 7 | 3.34 | 0.10 |
| Survival—Preemergent adults | | | |
| Test | 1, 3 | 0.01 | 0.91 |
| Temperature | 7, 3 | 16.72 | 0.02 |
| Relative humidity | 2, 5 | 20.49 | <0.01 |
| Survival—Egg to adult emergence | | | |
| Test | 1, 4 | 1.07 | 0.36 |
| Temperature | 8, 4 | 46.56 | <0.01 |
| Relative humidity | 2, 7 | 67.52 | <0.01 |
| Number of multiply-infested kernels | | | |
| Test | 1, 4 | 0.28 | 0.62 |
| Temperature | 8, 4 | 1.13 | 0.49 |
| Relative humidity | 2, 7 | 5.42 | 0.04 |
| Number of weevils per multiply-infested kernel | | | |
| Test | 1, 4 | 0.37 | 0.57 |
| Temperature | 8, 4 | 0.80 | 0.64 |
| Relative humidity | 2, 3 | 13.16 | 0.03 |
| Proportion survival in multiply-infested kernels | | | |
| Test | 1, 4 | 0.50 | 0.52 |
| Temperature | 8, 4 | 5.09 | 0.07 |
| Relative humidity | 2, 3 | 6.44 | 0.08 |
| Sex ratio | | | |
| Test | 1, 3 | 3.86 | 0.14 |
| Temperature | 5, 3 | 2.45 | 0.25 |
| Relative humidity | 2, 2 | 1.25 | 0.44 |

**Table 2. Duration of immature development of maize weevils reared at 30 ± 1°C and 75% RH on varying quantities of corn**

| Quantity of corn, g | Duration, wk |
|---|---|
| 32 | 4.78 ± 0.36a |
| 64 | 4.69 ± 0.24a |
| 128 | 4.84 ± 0.23a |
| 256 | 5.10 ± 0.26b |

Means ± SD followed by the same letter are not significantly different ($\alpha = 0.05$, $n = 15$ for each treatment level; ANOVA procedure, Waller–Duncan $k$-ratio test, SAS Institute 1987).

ment in that environment. The index was modified as number of progeny produced per 10 females, because I used different numbers of ovipositing females at different conditions. This index incorporates number of eggs laid, survival to the adult stage, and development time. Larger index values indicate greater suitability of the environment for maize weevil development. Dobie (1974) suggested that this index approaches the intrinsic rate of increase, $r_m$. TableCurve3D was used to fit an equation to the unweighted index versus temperature and relative humidity data.

## Results

**Density Optimization.** The grand mean of the moisture contents of the 300-g samples of equilibrated corn was 14.5% (SD = 0.28, $n$ = 113). The relationships of duration of immature development and number of progeny produced with quantity of corn provided were consistent over the three tests. That is, test by treatment interaction was not significantly different from the error mean square [duration by test interaction: $F$ = 1.84; df = 6, 48; $P(F > 1.84) = 0.11$; progeny by test interaction: $F = 1.18$; df = 6, 48; $P(F > 1.18) = 0.33$], so interaction and error mean square terms were combined to test for differences among treatments. Duration of immature development and number of progeny produced varied statistically with quantity of corn provided (Table 1). However, differences among treatment means for duration of development were not considered to be biologically significant (Table 2).

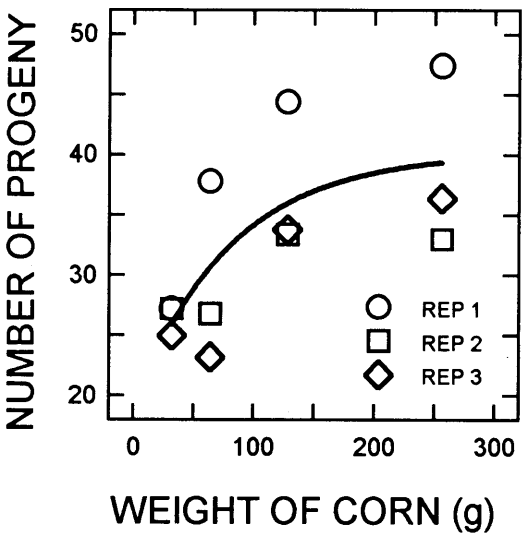


**Fig. 1.** Number of maize weevil progeny produced after five females oviposited for 24 h on varying quantities of corn at 30 ± 1°C and 75% RH (each symbol represents the mean of five cages). Solid line is an asymptotic curve fit (from equation 3) to the data.

**Table 3. Statistical analyses of equations**

| Equation | $R^2$ | Max $R^2$[a] | Lack of fit | | |
|---|---|---|---|---|---|
| | | | df | $F$ | $P > F$ |
| 3, Density | 0.50 | 0.51 | 1, 8 | 0.31 | 0.59 |
| 4, Moisture content | 0.99 | 1.00 | 24, 13 | 1.20 | 0.38 |
| 5, Development time | 0.98 | 0.98 | 7, 20 | 0.17 | 0.99 |
| 6, Fecundity | 0.87 | 0.97 | 22, 14 | 1.82 | 0.12 |
| 7, Survival | 0.82 | 0.98 | 22, 14 | 4.52 | <0.01[b] |
| 8, Susceptibility index | 0.93 | 0.99 | 21, 14 | 3.93 | 0.01[b] |

[a] Maximum $R^2$ indicates the maximum amount of variation that any equation fit to the data could explain, given the pure error in the data (Draper & Smith 1981). That is, no equation can explain differences in data measured at identical values of the independent variables.

[b] Although lack of fit is significant, response surfaces that fit the data better did not seem reasonable for describing the data.

The number of progeny produced increased as quantity of corn provided increased (Fig. 1). This relationship was described by the following asymptotic equation (Table 3):

$$\text{progeny} = \alpha + \beta e^{-\gamma(\text{weight})}, \qquad (3)$$

where progeny = number of progeny produced, weight = weight of corn (g), $\alpha$ = 40.21 (SE = 5.567), $\beta$ = −21.48 (8.562), and $\gamma$ = 0.01265 (0.01366). To be assured of being within four progeny of the asymptote ($\alpha$), with 95% confidence, between 30 and 236 g of corn should be provided to the weevils. Thus, 256 g of corn were provided to the weevils in the development rate test to minimize density effects.

**Sieving Frequency.** The grand mean of the moisture contents of the 300-g samples of corn was 14.6% (SD = 0.24, $n$ = 120). The relationships of number of progeny produced and duration of development with sieving frequency was consistent among tests. That is, test by treatment interaction was not significantly different from the error mean square [progeny by test interaction: $F$ = 1.36; df = 12, 78; $P(F > 1.36) = 0.20$; duration by test interaction: $F$ = 1.01; df = 12, 78; $P(F > 1.01) = 0.45$], so interaction and error mean squares were combined to test for differences among treatments. Neither number of progeny produced nor duration of development varied significantly with sieving frequency (Ta-

**Table 4. Number of progeny produced and duration of immature development of maize weevils reared at 30 ± 1°C and 75% RH when emerging adult progeny were sieved from the samples at various frequencies**

| Sieving frequency, d | No. progeny produced | | Duration of development, days | | n |
|---|---|---|---|---|---|
| | Mean ± SD | 95% CI | Mean ± SD | 95% CI | |
| 1 | 42.2 ± 13.8 | 38.9–45.7 | 33.8 ± 1.8 | 33.1–34.6 | 20 |
| 2 | 45.6 ± 14.1 | 42.1–49.1 | 33.9 ± 2.0 | 33.2–34.6 | 20 |
| 3 | 44.5 ± 15.2 | 41.0–48.0 | 34.0 ± 1.7 | 33.3–34.8 | 19 |
| 7 | 43.9 ± 12.9 | 40.4–47.4 | 34.0 ± 1.6 | 33.3–34.7 | 20 |
| 14 | 47.2 ± 18.1 | 43.7–50.7 | 33.5 ± 1.7 | 32.8–34.2 | 19 |

Neither number of progeny produced nor duration of development varied significantly with sieving frequency (Table 1).

bles 1 and 4). Thus, samples generally were sieved every day in the development rate test.

**Immature Development.** *Moisture Content.* Equilibrium moisture contents of the 300-g samples of corn at each environmental condition did not differ by >0.5% between tests. Given that the moisture tester is accurate to at worst ±0.5% over the range of temperatures and moisture contents studied (unpublished data), moisture content data from the two tests were combined for further analysis. Moisture content decreased with both increasing temperature within a relative humidity and with decreasing relative humidity within a temperature, as expected (Pixton & Warburton 1971).

The moisture contents predicted by the Chung-Pfost equation did not correlate well with moisture contents observed in the current study (Fig. 2). Parameters for the Chung-Pfost equation fit to my data were $a$ = 0.2738 (SE = 0.005349), $b$ = 0.03606 (0.0008928), and $c$ = 35.82 (4.732). The equation fit to my data was (Table 3):

$$MC = a - (b * T^2) + (c * RH), \qquad (4)$$

where $MC$ = % moisture content/100, $T$ = temperature (°C), $RH$ = % relative humidity/100, $a$ = 0.06246 (SE = 0.001194), $b$ = 0.00001274 (0.0000005548), and $c$ = 0.1229 (0.001857). Comparison of residual mean square errors (MSE) and residual patterns for the Chung-Pfost equation fit to my data (MSE = $6.39 \times 10^{-6}$) and for the new regression equation (MSE = $2.39 \times 10^{-6}$) indicated that the simpler equation fit the observed moisture content data better. The parameters $a$ and $b$ in equation 4 may be multiplied by 100 for direct input of percent moisture content and percent relative humidity, rather than inputting on a decimal basis.

*Duration of Development.* Although duration of development did not vary significantly between tests, the test by temperature interaction term was significant indicating that the response to temperature varied with test (Table 1). Development was more rapid in the second test (Table 5). Thus, data for the two tests were analyzed separately for differences between sexes. Duration of development did not vary significantly with sex in either test (Table 1).

Equations for predicting the effects of environmental conditions on duration of development were fit to data from the second test, because these data encompassed the widest range of temperatures at which some weevils completed development. The data are described by the equation (Table 3, Fig. 3):

$$\text{duration} = a + \frac{b}{\text{temp}^{0.5}} + c \log_e(\text{temp}) + de^{-\text{temp}} + \frac{f}{\text{RH}^2}, \qquad (5)$$

where $a$ = 5,546.58 (SE = 1,089.41), $b$ = −103,275 (19,896.7), $c$ = 117,477 (22,420.7), $d$ = $2.91121 \times 10^8$ ($2.04760 \times 10^7$), $e$ is the constant 2.71828, and $f$ = 81,979.0 (15,301.0). The equation was fit to unweighted duration data.

*Fecundity.* The number of eggs laid during the 24-h oviposition period (Table 6) did not differ significantly between tests, but did differ with temperature and relative humidity (Table 1). The data can be described by the equation (Table 3, Fig. 4):

$$\text{eggs} = \frac{a}{\left[1 + \left(\frac{\text{temp} - b}{c}\right)^2\right]\left[1 + \left(\frac{\text{RH} - d}{c}\right)^2\right]}, \qquad (6)$$

where $a$ = 330.550 (SE = 189.546), $b$ = 28.1315 (0.216622), $c$ =3.20929 (0.522826), and $d$ = 94.7541 (3.53407). The equation was fit to unweighted data.

*Survival.* Proportion survival (Table 7) of eggs, larvae, and pupae did not differ significantly between tests, among temperatures, or among relative humidities (Table 1). In general, proportion survival of eggs, larvae, and pupae was high (with little variability) from 17.5 to 32.5°C over NaCl and NaBr. Proportion survival of these stages was quite variable at higher and lower temperatures and at all temperatures over $K_2CO_3$. Proportion survival (Table 7) of preemergent adults (a stage where the adult has emerged from the pupal case, but has not emerged from the kernel) and proportion survival from egg to emerged adult did not differ significantly be-

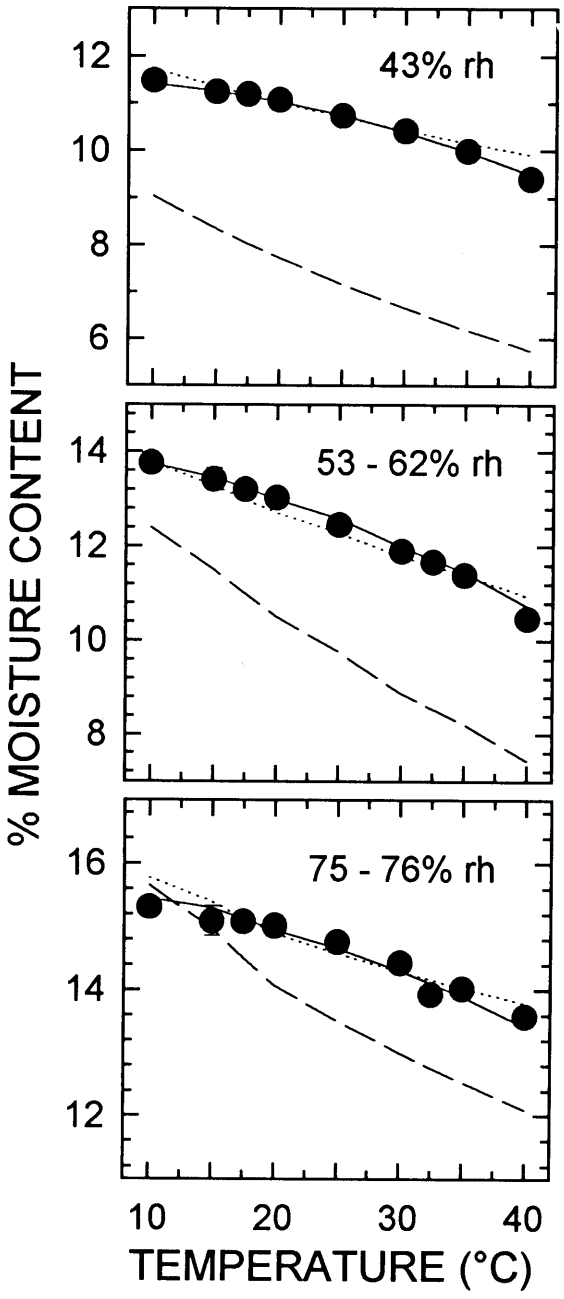


**Fig. 2.** Equilibrium moisture contents of 'Pioneer 3320' corn equilibrated at a range of temperatures and relative humidities: observed mean ± SD (solid circles), predicted using Chung-Pfost equation (long-dashed line), predicted using modified Chung-Pfost equation (short-dashed line), and predicted using a newly developed equation (solid line).

tween tests but did differ with temperature and relative humidity (Table 1). Survival from egg to adult emergence can be described by the equation (Table 3, Fig. 5):

$$\text{survival} = a + be^{-0.5\left[\left(\frac{\text{temp} - c}{d}\right)^2 + \left(\frac{\log_e\left(\frac{\text{RH}}{f}\right)}{g}\right)^2\right]}, \quad (7)$$

where: $a = -0.124731$ (SE = 0.086021), $b = 1.14602$ (0.0923718), $c = 25.0400$ (0.363540), $d = 6.58875$ (0.743550), $e$ is the constant 2.78128, $f = 68.3030$ (2.76308), and $g = 0.314531$ (0.0544211). The equation was fit to unweighted data.

*Multiply-Infested Kernels.* The number of kernels per cage that contained more than one weevil did not differ significantly between tests or with temperature, but did vary with relative humidity (Table 1). The mean number of multiply-infested kernels was 0.89 (SEM = 0.17, $n = 36$) at 43% RH, 0.60 (SEM = 0.14, $n = 42$) at 53–62% RH, and 1.33 (SEM = 0.23, $n = 42$) at 75–76% RH. The number of multiply-infested kernels in a cage was not correlated with the number of eggs laid in that cage [$r = 0.04$; $n = 111$; $P(r > 0.04) = 0.69$]. The number of weevils per multiply-infested kernel did not differ significantly between tests or with temperature, but did vary with relative humidity (Table 1). The number of weevils per multiply-infested kernel was 2.53 (SEM = 0.22, $n = 32$) at 43% RH, 2.04 (SEM = 0.04, $n = 25$) at 53–62% RH, and 2.36 (SEM = 0.13, $n = 56$) at 75–76% RH. The proportion survival of weevils in multiply-infested kernels did not differ significantly between tests, with temperature, or with relative humidity (Table 1). The proportion survival of weevils in multiply-infested kernels was 0.18 (SEM = 0.03, $n = 113$).

*Sex Ratio.* The female proportion of emerging progeny did not vary significantly with test, temperature, or relative humidity (Table 1). The mean proportion of females in all cages was 0.46, which did not differ significantly from a 1:1 sex ratio (SEM = 0.026, $n = 59$, 95% confidence interval = 0.40 to 0.51).

*Index of Susceptibility.* The Dobie index of susceptibility indicated that weevil development was optimal at 25°C at 43% RH, and at 30°C at 53–62% RH and 75–76% RH (Fig. 6). Below optimal temperatures, environmental suitability dropped gradually. Above optimal temperatures, environmental suitability dropped rapidly. At optimal relative humidity (75%), environmental suitability dropped from nearly optimal at 32.5°C to totally unsuitable at 35°C. The relationship between the Dobie index of susceptibility and temperature and relative humidity can be described by the equation (Table 3, Fig. 6):

$$\text{index} = e^{[a + b\log_e(\text{temp}) + \frac{c}{\text{temp}^{0.5}} + \frac{d}{\text{temp}} + \frac{f\log_e \text{temp}}{\text{temp}^2} + \frac{g}{\text{RH}^2}]}, \quad (8)$$

**Table 5. Mean and median of duration of immature development of maize weevils (in days), number of adult progeny produced per cage, and number of cages in which adult progeny emerged in corn at various temperatures and relative humidities in two tests**

| Temp, °C | Test 1 | | | | Test 2 | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean duration[a] | Median[b] | No. progeny[c] | No. cages[d] | Mean duration[a] | Median[b] | No. progeny[c] | No. cages[d] |
| | | | | 43% RH | | | | |
| 20 | 115.0 ± 25.5[e,f] | 115.0 ± — | 2.0 ± — | 1 | —[g] | —[g] | —[g] | —[g] |
| 25 | 64.9 ± 5.3 | 64.3 ± 6.4 | 2.7 ± 1.2 | 3 | —[g] | —[g] | —[g] | —[g] |
| | | | | 53–62% RH | | | | |
| 17.5 | —[h] | —[h] | —[h] | —[h] | 103.6 ± 1.8 | 100.2 ± 3.5 | 7.3 ± 4.0 | 3 |
| 20 | 77.2 ± 12.3 | 70.8 ± 7.5 | 13.7 ± 5.1 | 3 | 76.5 ± 3.3 | 73.2 ± 3.4 | 20.0 ± 5.6 | 3 |
| 25 | 50.2 ± 2.6 | 49.0 ± 1.3 | 15.0 ± 3.0 | 3 | 39.7 ± 2.3 | 38.3 ± 0.6 | 25.7 ± 4.2 | 3 |
| 30 | 39.6 ± 1.2 | 38.0 ± 2.2 | 15.3 ± 9.0 | 3 | 33.4 ± 3.0 | 32.0 ± 2.6 | 16.3 ± 4.2 | 3 |
| 32.5 | —[h] | —[h] | —[h] | —[h] | 41.1 ± 0.4[i] | 40.0 ± 2.8 | 7.0 ± 0.0 | 2 |
| | | | | 75–76% RH | | | | |
| 15 | 203.2 ± 45.5[e,j] | 205.5 ± — | 3.0 ± — | 1 | 193.6 ± 25.1 | 191.7 ± 28.1 | 4.3 ± 2.1 | 3 |
| 17.5 | —[h] | —[h] | —[h] | —[h] | 93.3 ± 4.0 | 93.8 ± 5.5 | 19.7 ± 2.9 | 3 |
| 20 | 64.4 ± 1.1 | 61.8 ± 1.4 | 12.3 ± 4.9 | 3 | 63.7 ± 8.5[e,k] | 63.0 ± — | 38.0 ± — | 1 |
| 25 | 40.2 ± 1.9 | 39.3 ± 2.1 | 34.0 ± 2.6 | 3 | 32.9 ± 1.0 | 32.0 ± 1.0 | 51.3 ± 2.3 | 3 |
| 30 | 31.9 ± 0.8 | 30.7 ± 1.2 | 55.3 ± 8.5 | 3 | 26.3 ± 0.2 | 25.7 ± 0.6 | 48.0 ± 15.7 | 3 |
| 32.5 | —[h] | —[h] | —[h] | —[h] | 30.0 ± 0.2 | 28.5 ± 0.9 | 47.3 ± 8.5 | 3 |

[a] Mean ± SD of the mean duration of development of weevils emerging in up to three cages (as indicated in number of cages column). Because this is a mean of up to three means, the standard deviation is an estimate of the standard deviation of the mean (Steel & Torrie 1960, p. 56). Multiply the standard deviation by the square root of the number of cages to obtain an estimated standard deviation for simulating variation in development rate.

[b] Mean ± SD of the median duration of development of weevils emerging in up to three cages (as indicated in no. cages column).

[c] Mean ± SD of the number of adult progeny emerging in up to three cages (as indicated in number of cages column).

[d] Number of cages (up to three) in which at least one adult progeny emerged.

[e] Because data for progeny emerging in only one cage are used, this standard deviation is for the progeny emerging in that one cage. Other standard deviations are for the means of three cages.

[f] Data from one cage in which one male emerged were not used in the analysis because the day that the one male emerged was not determined.

[g] No weevils emerged at these conditions in this test.

[h] This temperature/relative humidity combination was not tested.

[i] Data for one cage were not used in the analysis because one adult female was removed on day 7.

[j] Data for one cage were not used in the analysis because two live adults were present in dissected kernels on day 308.

[k] Data for two cages were not used in the analysis because one male emerged in one cage and one male and three females emerged in another cage before daily sieving was begun.

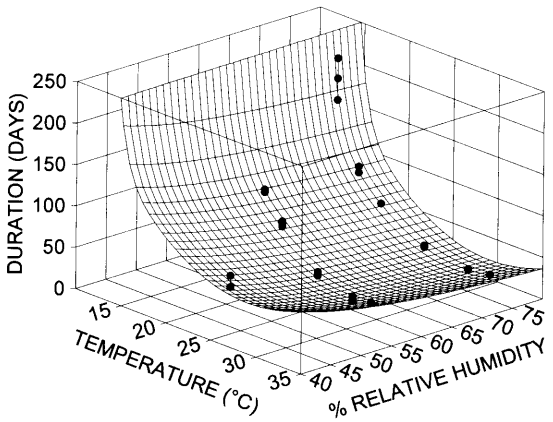


**Fig. 3.** Mean observed (circles) and predicted (response surface from equation 5) duration of development of maize weevils reared at various temperatures and relative humidities in the second test. Solid lines indicate distance of observed means from the response surface.

**Table 6. Number of eggs laid per female maize weevil during a 24-h oviposition period in corn at various temperatures and relative humidities**

| Temp, °C | Total no. eggs/no. females/24 h, mean ± SD (*n*) | | |
|---|---|---|---|
| | 43% RH | 53–62% RH | 75–76% RH |
| 10 | 0.28 ± 0.48 (3)[a] | 0.39 ± 0.42 (3)[a] | 0.19 ± 0.17 (3)[a] |
| 15 | 0.14 ± 0.12 (2) | 0.26 ± 0.06 (2) | 0.55 ± 0.09 (2) |
| 17.5 | 0.29 ± 0.28 (3)[a] | 0.74 ± 0.10 (3)[a] | 1.29 ± 0.18 (3)[a] |
| 20 | 0.33 ± 0.18 (2) | 1.54 ± 0.31 (2) | 2.31 ± 0.30 (2) |
| 25 | 0.41 ± 0.03 (2) | 1.61 ± 0.03 (2) | 4.06 ± 0.05 (2) |
| 30 | 0.41 ± 0.30 (2) | 1.75 ± 0.82 (2) | 6.65 ± 1.48 (2) |
| 32.5 | —[b] | 0.68 ± 0.04 (3)[a] | 3.05 ± 0.51 (3)[a] |
| 35 | 0.46 ± 0.76 (3)[a] | 0.15 ± 0.00 (2) | 0.42 ± 0.59 (2) |
| 40 | 0.18 ± 0.31 (3)[a] | 0.30 ± 0.25 (3)[a] | 0.34 ± 0.60 (3)[a] |

[a] This is the mean and standard deviation for data from just one replications of the test over time, because this environmental condition was tested in just one replication of the test. *n*, Number of test cages in that one replication.

[b] This combination of environmental conditions was not tested.

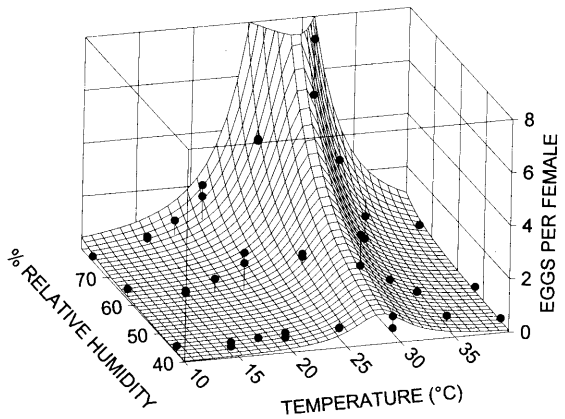


**Fig. 4.** Mean observed (circles) and predicted (response surface from equation 6) number of eggs laid per female maize weevil (total number of eggs/number of females) during a 24-h oviposition period when reared at various temperatures and relative humidities. Solid lines indicate distance of observed means from the response surface.

where $a$ = 19,696.6 (SE = 449.501), $b$ = −2,889.20 (72.7361), $c$ = −83,408.9 (1,422.39), $d$ = 187,391 (1,728.55), $e$ is the constant 2.71828, $f$ = −235,431 (0.0000), and $g$ = −5,985.48 (644.539).

## Discussion

**Density.** A systematic study of the effects of density on duration of development of maize weevils has not been reported before. However, Birch (1945) showed that duration of immature development of rice weevils was longer when more than one egg was deposited in a kernel of wheat. When more than one weevil larva occurs in a wheat kernel, usually the largest larva will eat the smaller larvae (Sharifi & Mills 1971). Thus, the effect of density on duration of development appears to be due to competition between larvae within a grain kernel. Experimental designs that minimize the number of multiply-infested kernels would be expected to minimize the duration of development. Over the range of densities that I studied (five females ovipositing for 48 h on 32–256 g of corn), differences in duration of development were not biologically significant. Differences in number of progeny produced were significant. Differences in number of progeny produced may result from differences in numbers of eggs laid or from differences in survivorship, or both. Thus, when density is not optimized, data obtained on numbers of progeny produced may be misleading (see Baker et al. 1991b for discussion).

My results indicating that density does not affect duration of development should not be extrapolated to most previous studies on duration of maize weevil development because densities in those studies were almost always higher than the highest densities that I tested. Thus, more multiply-infested kernels and longer development times would be expected in those studies. Also, my results on corn may not be applicable to other grains because equal amounts of different grains may not provide the same nutrition. Hwang et al. (1983) used 15 females ovipositing for 48 h on 200 rice grains (=3.66 g [Baker et al. 1991a]), a density ≈26 times higher than the highest density that I tested. Chesnut & Douglas (1971) used five females ovipositing for 24 h on five kernels of corn, a density ≈10 times higher than the highest density I tested. Satomi (1960) used 100 unsexed weevils ovipositing for 24 h on 150 g of rice, a density about equal to the highest density I tested. Howe (1952) placed one female on one wheat grain for 24 h and averaged two insects per kernel, a condition that he acknowledged affects development time. Birch (1944) chose wheat kernels containing only one egg, and, thus, was able to avoid problems with density effects.

**Sieving Frequency.** Ungsunantwiwat & Mills (1979) reported that sieving frequency affected the number of progeny produced by an Arkansas strain of the maize weevil, but not by a Mexican strain. I found no difference in number of progeny produced or duration of development at sieving frequencies from 1 to 14 d. Ungsunantwiwat & Mills (1979) sieved their samples ≈55 times in 15 s. I sieved vigorously for 3–4 s, held samples stationary for a few seconds, and sieved again. Differences in sieving may explain the differences in results between the two studies.

There are no previous reports on the effects of observation frequency on duration of development of maize weevils. However, Bailey (1969) showed that dropping grain containing immature stages of a related species, the granary weevil, *S. granarius* (L.), did not affect duration of development. The impact either killed the insects or they continued developing at the normal rate. He showed that impact had the greatest effect on mortality of prepupae and pupae.

**Immature Development.** *Duration of Development.* The effects of temperature on duration of development varied between tests. The two tests were conducted 1 yr apart. Thus, differences may have resulted from variation in the weevils or in the corn used. We collect weevils from three sites in South Carolina and add progeny from these weevils to our culture monthly. Doing so maximizes variation in the culture and keeps the culture as close to a field strain as possible, but also may change the genetic makeup of the culture. Satomi (1960) found the duration of development of four geographic

**Table 7. Number entering each stage (mean of two tests ± SD) and proportion survivorship through the stage (mean ± SD) of maize weevils in corn at various temperatures and relative humidities**

| Stage | Temp, °C | 43% RH | | | 53–62% RH | | | 75–76% RH | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | No. entering stage | Proportion Survivorship | *n* | No. entering stage | Proportion Survivorship | *n* | No. entering stage | Proportion Survivorship | *n* |
| Egg | 10 | 5.15 ± 4.16 | 1.00 ± 0.00 | 2[a] | 6.33 ± 2.50 | 0.71 ± 0.19 | 2[a] | 2.45 ± 0.93 | 0.71 ± 0.19 | 3[a] |
| | 15 | 2.71 ± 1.64 | 0.67 ± 0.46 | 2 | 4.94 ± 1.96 | 0.65 ± 0.50 | 2 | 9.73 ± 4.19 | 0.69 ± 0.36 | 2 |
| | 17.5 | 6.28 ± 3.06 | 0.29 ± 0.18 | 3[a] | 14.92 ± 1.24 | 0.62 ± 0.15 | 3[a] | 25.83 ± 2.03 | 0.81 ± 0.03 | 3[a] |
| | 20 | 5.20 ± 1.52 | 0.62 ± 0.12 | 2 | 23.18 ± 5.31 | 0.83 ± 0.00 | 2 | 36.95 ± 19.17 | 0.70 ± 0.15 | 2 |
| | 25 | 7.51 ± 1.34 | 0.91 ± 0.13 | 2 | 25.18 ± 10.59 | 0.89 ± 0.05 | 2 | 51.52 ± 13.02 | 0.89 ± 0.04 | 2 |
| | 30 | 5.83 ± 1.83 | 0.50 ± 0.11 | 2 | 24.78 ± 0.89 | 0.75 ± 0.11 | 2 | 65.60 ± 13.40 | 0.82 ± 0.08 | 2 |
| | 32.5 | —[b] | —[b] | —[b] | 21.37 ± 7.47 | 0.59 ± 0.01 | 3[a] | 61.18 ± 5.96 | 0.83 ± 0.02 | 3[a] |
| | 35 | 5.33 ± 4.43 | 0.65 ± 0.17 | 3[a] | 3.86 ± 1.82 | 0.62 ± 0.11 | 2 | 5.02 ± 6.50 | 0.61 ± 0.42 | 2 |
| | 40 | 3.34 ± 1.36 | 1.00 ± 0.00 | 3[a] | 5.11 ± 1.47 | 1.00 ± 0.00 | 3[a] | 6.36 ± 4.80 | 0.33 ± 0.13 | 2[a] |
| Larva | 10 | 5.15 ± 4.16 | 0.34 ± 0.34 | 2[a] | 4.99 ± 3.00 | 0.21 ± 0.13 | 2[a] | 1.55 ± 0.72 | 0.64 ± 0.22 | 3[a] |
| | 15 | 2.38 ± 2.11 | 0.53 ± 0.58 | 2 | 3.81 ± 0.35 | 0.22 ± 0.15 | 2 | 6.21 ± 0.19 | 0.65 ± 0.37 | 2 |
| | 17.5 | 0.99 ± 0.59 | 0.33 ± 0.33 | 3[a] | 9.63 ± 3.21 | 0.99 ± 0.00 | 3[a] | 20.87 ± 1.53 | 0.99 ± 0.00 | 3[a] |
| | 20 | 2.94 ± 0.32 | 0.75 ± 0.27 | 2 | 19.11 ± 4.52 | 0.98 ± 0.02 | 2 | 27.72 ± 19.09 | 0.97 ± 0.00 | 2 |
| | 25 | 6.91 ± 0.49 | 0.70 ± 0.06 | 2 | 22.08 ± 8.42 | 0.96 ± 0.01 | 2 | 45.95 ± 13.41 | 0.95 ± 0.03 | 2 |
| | 30 | 3.42 ± 3.42 | 0.52 ± 0.16 | 2 | 18.88 ± 0.91 | 0.95 ± 0.06 | 2 | 53.70 ± 5.46 | 0.98 ± 0.00 | 2 |
| | 32.5 | —[b] | —[b] | —[b] | 12.74 ± 4.64 | 0.91 ± 0.04 | 3[a] | 50.88 ± 4.14 | 0.97 ± 0.00 | 3[a] |
| | 35 | 2.77 ± 2.28 | 0.33 ± 0.33 | 3[a] | 0.83 ± 0.46 | 0.33 ± 0.23 | 2 | 1.74 ± 2.00 | 0.22 ± 0.16 | 2 |
| | 40 | 3.34 ± 1.36 | 0.37 ± 0.32 | 3[a] | 5.11 ± 1.47 | 0.08 ± 0.08 | 3[a] | 1.51 ± 0.80 | 0.50 ± 0.50 | 2[a] |
| Pupa | 10 | 0.67 ± — | 0.00 ± — | 1[a] | 0.67 ± 0.00 | 0.00 ± 0.00 | 2[a] | 0.67 ± 0.00 | 0.00 ± 0.00 | 3[a] |
| | 15 | 0.75 ± 0.11 | 0.25 ± 0.35 | 2 | 0.91 ± 0.01 | 0.59 ± 0.59 | 2 | 3.92 ± 1.96 | 0.83 ± 0.24 | 2 |
| | 17.5 | 0.76 ± — | 0.00 ± — | 1[a] | 9.52 ± 3.21 | 0.96 ± 0.04 | 3[a] | 20.76 ± 1.53 | 0.95 ± 0.02 | 3[a] |
| | 20 | 2.00 ± 0.86 | 0.52 ± 0.58 | 2 | 18.86 ± 4.78 | 1.00 ± 0.00 | 2 | 26.61 ± 18.62 | 0.96 ± 0.05 | 2 |
| | 25 | 4.77 ± 1.06 | 0.87 ± 0.15 | 2 | 21.33 ± 7.98 | 0.99 ± 0.02 | 2 | 43.30 ± 11.37 | 0.99 ± 0.01 | 2 |
| | 30 | 1.22 ± 0.26 | 0.63 ± 0.53 | 2 | 17.81 ± 2.38 | 0.99 ± 0.00 | 2 | 52.71 ± 5.16 | 0.99 ± 0.01 | 2 |
| | 32.5 | —[b] | —[b] | —[b] | 11.97 ± 4.97 | 1.00 ± 0.00 | 3[a] | 49.11 ± 3.85 | 0.97 ± 0.02 | 3[a] |
| | 35 | 0.67 ± — | 0.00 ± — | 1[a] | 0.79 ± 0.16 | 0.50 ± 0.71 | 2 | 0.72 ± 0.06 | 0.00 ± 0.00 | 2 |
| | 40 | 1.20 ± 0.48 | 0.50 ± 0.50 | 2[a] | 1.39 ± — | 0.51 ± — | 1[a] | 0.72 ± — | 1.00 ± — | 1[a] |
| Adult in kernel | 15 | 0.91 ± — | 0.00 ± — | 1[a] | 0.81 ± 0.13 | 0.00 ± 0.00 | 2 | 3.58 ± 2.44 | 0.69 ± 0.27 | 2 |
| | 17.5 | —[c] | —[c] | —[c] | 9.27 ± 3.36 | 0.83 ± 0.09 | 3[a] | 19.67 ± 1.67 | 1.00 ± 0.00 | 3[a] |
| | 20 | 1.64 ± 1.04 | 0.22 ± 0.31 | 2 | 18.86 ± 4.78 | 0.88 ± 0.03 | 2 | 25.80 ± 19.05 | 0.99 ± 0.01 | 2 |
| | 25 | 4.09 ± 1.67 | 0.80 ± 0.16 | 2 | 21.10 ± 8.29 | 0.97 ± 0.02 | 2 | 43.07 ± 11.68 | 0.99 ± 0.02 | 2 |
| | 30 | 1.06 ± 0.49 | 0.13 ± 0.19 | 2 | 17.57 ± 2.36 | 0.91 ± 0.09 | 2 | 52.10 ± 5.38 | 0.99 ± 0.01 | 2 |
| | 32.5 | —[b] | —[b] | —[b] | 11.97 ± 4.97 | 0.97 ± 0.03 | 3[a] | 47.94 ± 4.65 | 0.99 ± 0.01 | 3[a] |
| | 35 | —[c] | —[c] | —[c] | 0.91 ± — | 0.00 ± — | 1[a] | —[c] | —[c] | —[c] |
| | 40 | 0.72 ± — | 0.00 ± — | 1[a] | 0.72 ± — | 0.00 ± — | 1[a] | 0.72 ± — | 0.00 ± — | 1[a] |
| Egg to adult | 10 | 5.15 ± 4.16 | 0.00 ± 0.00 | 2[a] | 6.33 ± 2.50 | 0.00 ± 0.00 | 2[a] | 2.45 ± 0.93 | 0.00 ± 0.00 | 3[a] |
| | 15 | 2.71 ± 1.64 | 0.00 ± 0.00 | 2 | 4.94 ± 1.96 | 0.00 ± 0.00 | 2 | 9.73 ± 4.19 | 0.27 ± 0.11 | 2 |
| | 17.5 | 6.28 ± 3.06 | 0.00 ± 0.00 | 3[a] | 14.92 ± 1.24 | 0.47 ± 0.11 | 3[a] | 25.83 ± 2.03 | 0.76 ± 0.04 | 3[a] |
| | 20 | 5.20 ± 1.52 | 0.12 ± 0.17 | 2 | 23.18 ± 5.31 | 0.72 ± 0.04 | 2 | 36.95 ± 19.17 | 0.64 ± 0.16 | 2 |
| | 25 | 7.51 ± 1.34 | 0.38 ± 0.03 | 2 | 25.18 ± 10.59 | 0.82 ± 0.05 | 2 | 51.52 ± 13.02 | 0.83 ± 0.03 | 2 |
| | 30 | 5.83 ± 1.83 | 0.09 ± 0.12 | 2 | 24.78 ± 0.89 | 0.64 ± 0.09 | 2 | 65.60 ± 13.40 | 0.79 ± 0.08 | 2 |
| | 32.5 | —[b] | —[b] | —[b] | 21.37 ± 7.47 | 0.52 ± 0.02 | 3[a] | 61.18 ± 5.96 | 0.77 ± 0.01 | 3[a] |
| | 35 | 5.33 ± 4.43 | 0.00 ± 0.00 | 3[a] | 3.86 ± 1.82 | 0.00 ± 0.00 | 2 | 5.02 ± 6.50 | 0.00 ± 0.00 | 2 |
| | 40 | 3.34 ± 1.36 | 0.00 ± 0.00 | 3[a] | 5.11 ± 1.47 | 0.00 ± 0.00 | 3[a] | 6.36 ± 4.80 | 0.00 ± 0.00 | 2[a] |

[a] Mean and standard error of the mean for data from just one test, because this environmental condition was tested in just one test. *n*, Number of cages in the one test in which some individuals entered this stage.
[b] This combination of environmental conditions was not tested.
[c] No insects survived to this stage at these environmental conditions.

strains of the maize weevil to differ little, 3–4 d at 20–30°C.

I used corn for the two tests from two different crop years, but it was the same variety and grown in the same region. Classen et al. (1990) showed that the Dobie index of susceptibility (which includes duration of development) was correlated with ferulic acid content of corn. Number of eggs laid and number of progeny produced were correlated with protein content of the corn. Thus, the differences I observed in duration of development may have been related to differences in chemistry of the two lots of corn. Unfortunately, I did not retain samples of the 1987 corn, and, thus, was unable to test for differences between the two lots.

I found no difference in duration of immature development of the two sexes. Satomi (1960) also found that sex did not affect duration of immature development in four geographical strains of the

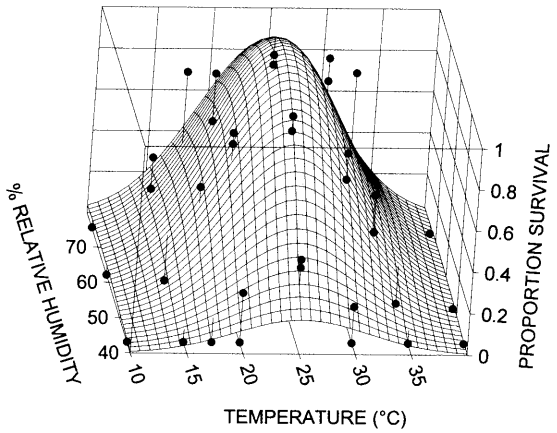


**Fig. 5.** Mean observed (circles) and predicted (response surface from equation 7) proportion survival from egg to adult emergence of maize weevils when reared at various temperatures and relative humidities. Solid lines indicate distance of observed means from the response surface.

maize weevil. Thus, sex does not need to be included as a factor when modeling development of immature maize weevils.

Results from previous studies on duration of immature development are not easily compared because environmental conditions varied among studies. Chesnut & Douglas (1971) reported on duration of immature development on corn, but did not specify which stages were measured. Presumably, they measured from oviposition to emergence of the adult from the kernel. Oddly, at 70 and 80% RH, development was more rapid

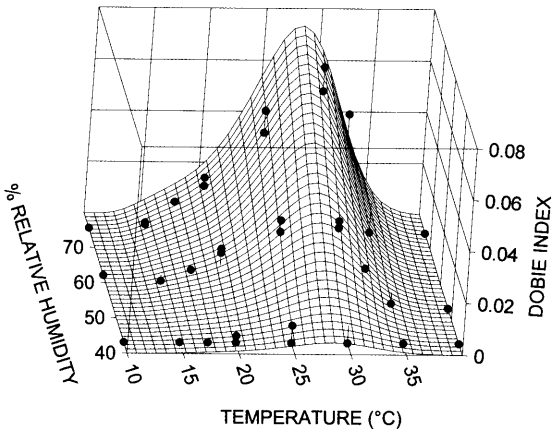


**Fig. 6.** Mean observed (circles) and predicted (response surface) index (Dobie 1974) indicating suitability of various environmental conditions for development of maize weevils. The index incorporates fecundity, survivorship, and development time. Increasing index values indicate increasing environmental suitability. Solid lines indicate distance of observed means from the response surface.

at 21.1°C than at 26.6°C in their study. Development at 70–80% RH and 26.6 and 32.2°C was similar to results from my study: ≈42 d at 26.6°C and ≈30 d at 32.2°C. At 15.5 and 21.1°C, they reported short development times of 52 and 39 d, respectively, compared with ≈200 d at 15°C and 64 d at 20°C in my study. Studies by Hwang et al. (1983) and Howe (1952) on rice and wheat also indicate much longer development times than reported by Chesnut & Douglas (1971). In all of these studies, duration of immature development was minimized at 28–32°C and generally increased as relative humidity decreased. The differences in development times between studies may be due to differences in weevils, grain type, variety, or experimental design.

*Sex Ratio.* A 1:1 sex ratio was in agreement with that observed by Ungsunantwiwat & Mills (1979) for laboratory-reared weevils. Dix & All (1985) reported that weevils colonizing corn in the field were predominately males, but that their progeny and laboratory-reared weevils were predominately female.

*Fecundity.* Maximum daily fecundity (6.65 eggs per female in 24 h) was at 30°C and 75% RH. I calculated rates of daily fecundity from the Chesnut & Douglas (1971) data. Assuming a 1:1 sex ratio, the optimal conditions for fecundity were 26.6°C and 70% RH (3.04 eggs per female per 24 h). Differences in fecundity rates between the two studies probably resulted from differences in parental density, the weevil strains used, grain type, or experimental design. Other studies have not reported maize weevil fecundity over a range of environmental conditions; therefore, determination of optimal conditions for fecundity is not possible.

The intent of this study was not to quantify fecundity. Hence, rates reported here are the maximum that would be expected at any environmental condition. Actual rates would vary with age of the ovipositing female. My reported variations in fecundity also do not apply on a per-female basis, because I always had more than one female per cage to optimize the number of weevils emerging in a cage.

*Survival.* Chesnut & Douglas (1971) reported that the lower limit for development from egg to emergence of adult maize weevils was <15.6°C. I had a few weevils emerge at 15°C, but this was clearly an extreme condition for oviposition and development. Hwang et al. (1983) had no weevils emerge at any relative humidity at 13°C. Thus, the lower limit for survival from egg to adult emergence is between 13 and 15°C. Survival was high in my study from 17.5 to 32.5°C at 75% RH and from 20 to 30°C at 57% RH. Previous studies did not determine survival rates over a range of environmental conditions. No weevils survived to the adult stage at 35°C in my study. Hwang et al. (1983) had only a few survivors at 35°C and 60–75% RH. Few progeny survived to

the adult stage at or below 45% RH, with no survival at <20 or 32°C at 45% RH (Hwang et al. 1983, present study).

*Index of Susceptibility.* The Dobie index of susceptibility indicates the suitability of a given environment for population development because it incorporates oviposition, survival, and development time. Optimal environmental conditions for maize weevils on rice were 28°C and 85% RH, although the rice rotted at these conditions (Hwang et al. 1983). Thus, the rice would support maize weevil populations for only a short time. My results for corn were consistent with those for rice: optimal environmental conditions were 30°C and 75% RH.

Optimal storage conditions for avoiding maize weevil damage can be determined from Fig. 6 or from equation 8. Maize weevils will not complete development in grain stored at <15°C or ≥35°C. Population growth would be low at 43% RH or below at any temperature. Intermediate combinations of temperature and relative humidity can be chosen from Fig. 6 that would slow maize weevil population growth. Once complete fecundity data for maize weevils become available, a simulation model can then be used to further optimize maize weevil control strategies.

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