

POPULATION ECOLOGY

Size Preference and Sex Ratio for *Pteromalus cerealellae* (Hymenoptera: Pteromalidae) Parasitizing *Sitotroga cerealella* (Lepidoptera: Gelechiidae) in Stored Corn

BIRAN WEN,¹ DAVID K. WEAVER,² AND JOHN H. BROWER³

Stored-Product Insects Research and Development Laboratory, USDA-ARS,
3401 Edwin Street, Savannah, GA 31405

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ABSTRACT Hosts ranging from small larvae to pupae of the Angoumois grain moth, *Sitotroga cerealella* (Olivier), were exposed to females of the pteromalid parasitoid, *Pteromalus cerealellae* (Ashmead), to determine the effects of host size on preference, parasitism success, adult size, and progeny sex ratio of the parasitoid. The parasitoid successfully parasitized larvae (>0.43 mm in maximum body width), prepupae (1.55 ± 0.05 mm [mean \pm SEM] mm maximum average body width), and a single pupa (1.20 mm maximum body width). All female parasitoid progeny emerged from hosts that had a maximum body width >0.85 mm. Sixty-four percent of male parasitoid progeny emerged from hosts that had a maximum body width between 0.43 and 0.85 mm. Size of *P. cerealellae* adults was correlated with host size (larger parasitoids developed on larger hosts). The optimal host sizes for producing female parasitoid progeny were larvae with a maximum body width between 1.69 and 2.05 mm and prepupae. The optimal host sizes for producing male parasitoid progeny were larvae with a maximum body width between 0.57 and 0.70 mm. These results are discussed in terms of maximizing potential biological control of the Angoumois grain moth by this parasitoid.

KEY WORDS *Sitotroga cerealella*, *Pteromalus cerealellae*, host size preference, parasitoid, sex ratio

HOST SIZE IS one of several environmental factors that can influence parasitoid preference, fecundity, and development time (for example, Liu 1985, Opp and Luck 1986, Putters and van den Assem 1988, Bai 1992, Smith 1993). In some species there is a direct relationship between progeny size and size of the host on which they developed (for example, Charnov et al. 1981, Opp and Luck 1986, Tillman and Cate 1993). Host size also influences the sex ratio of many parasitoids, such that a female-biased sex ratio is produced on large hosts and a male-biased sex ratio is produced on small hosts (Flanders 1965; Crozier 1977; Charnov 1982; Waage 1986; King 1987, 1991, 1993).

Pteromalus [*Habrocytus*] *cerealellae* (Ashmead) is a solitary ectoparasitoid of the Angoumois grain moth, *Sitotroga cerealella* (Olivier). Females of this parasitoid lay eggs on immature Angoumois grain moths within kernels of grain. Nobel (1932) and

Fulton (1933) studied the parasitoid biology on the Angoumois grain moth, and Brower (1991) reported that this parasitoid attacked and successfully developed on 12 species of stored-product beetles in a no-choice situation. This oligophagy indicates it may have potential as a biological control agent for several important stored-product pests. Laboratory studies showed that this parasitoid has the potential to suppress Angoumois grain moth populations in stored corn (Wen and Brower 1994). However, there are no reports on the effect of size of this host on the parasitoid *P. cerealellae*, which is an important factor in determining host-parasitoid population dynamics (Bellows and Hassell 1988). The purpose of the current study was to investigate the effects of size of *S. cerealella* in corn on preference in host selection, parasitism success, size of adult progeny, and progeny sex ratio of the parasitoid *P. cerealellae*.

Materials and Methods

Source of Host, Parasitoid, and Corn Variety.

The culture of *P. cerealellae* originated from a field collection on *S. cerealella* in wheat from Eagle Pass, TX, in 1984. It has been cultured since that time in the USDA laboratory in Savannah on *S. cerealella* reared in wheat. Zero- to 1-d-old female

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¹Current address: Department of Entomology, University of Georgia, 413 Biological Science Building, Athens, GA 30602.

²Current address: Insect Attractants, Behavior, and Basic Biology Research Laboratory, USDA-ARS, P.O. Box 14565, Gainesville, FL 32604.

³Current address: U.S. Grain Marketing Research Laboratory, USDA-ARS, 1515 College Avenue, Manhattan, KS 66502.

P. cerealellae were collected by aspirating them from stock cultures and were placed in empty jars for 2 d to mate with males. Two- to 3-d-old female *P. cerealellae* were used for this experiment. Corn used in the experiment was 'Pioneer 3320'. All experiments were conducted at $25 \pm 0.5^\circ\text{C}$, $65 \pm 5\%$ RH, and a photoperiod of 12:12 (L:D) h.

Hosts were 1st-generation *S. cerealella* from adults collected on farm-stored corn in South Carolina. Parental *S. cerealella* were reared on Pioneer 3320 at $25 \pm 1^\circ\text{C}$, $65 \pm 5\%$ RH, and a photoperiod of 12:12 (L:D) h. Zero- to 1-d-old adults of *S. cerealella* were exposed to corn.

Host Size Preparation. Corn (200 g) was exposed to 10 pairs of *S. cerealella* for 2 d at 12 consecutive intervals. For each interval, 600 g of corn were exposed. On the 31st d after 1st infestation, the host ages from the 12 infestations were 29–31, 27–29, 25–27, 23–25, 21–23, 19–21, 17–19, 15–17, 13–15, 11–13, and 9–11 d old, respectively. This infested corn was used to determine both host size preference and parasitism success.

Host Size Preference. A 100 g corn sample was taken from each of the 12 infestation intervals. The 12 samples were mixed thoroughly in a large container. Seven 120-g samples from the mixed corn were weighed and placed in quart jars. On the 31st d after the 1st corn infestation, each 120-g sample was exposed to a single female *P. cerealellae* for 24 h. The parasitoid was then removed, and the corn was separated into three 40-g subsamples, glued to 3 sheets of film, and radiographed (Industrex M film [Ready pack II; Eastman Kodak, Rochester, NY]). The samples were exposed in a Faxitron (model 43855A; Hewlett-Packard, McMinnville, OR) at 28 kVp for 52 s. Radiographs were developed and observed at $20\times$ with a dissecting microscope. Maximum host body width was measured by using an ocular micrometer (± 0.024 mm precision). Infested corn kernels were removed from the film sheets and placed individually in small vials (6 by 1.5 cm) with sponge plugs. Emergence of parasitoids or adult hosts was recorded daily. If there was no emergence of either parasitoid or host, the corn kernel was dissected to determine if the hosts were parasitized and the fate of the host. Emerging parasitoids were stored in a freezer for 1 d after determining their sex. Head width of adult parasitoids was measured by using the same method that was used for measuring host size; head width was used as an index of parasitoid size.

Parasitism Success. Corn and hosts (29–31, 25–27, 21–23, 17–19, 13–15, and 9–11 d old) were used for this experiment. On the 30th d after the 1st infestation, four 40-g samples from each of the 6 infestations were taken to determine host density by radiography. The number of hosts in each sample was counted by observing the radiographs with a dissecting microscope. Depending on host density, corn in each sample was diluted, if necessary, to a similar host density. However, because some

hosts (9–11 and 13–15 d old) were too small to determine the total host density, these dilutions were made according to the average density of the other 4 infestations. On the 31st d after the 1st corn infestation, six 80-g samples were taken from each of 6 infestations, and each sample was exposed to 1 female *P. cerealellae* for 24 h, after which the females were removed. After these parental parasitoids were removed, four 40-g samples of undiluted corn from each of 6 different host exposure periods were taken and radiographed. Average host size for each host exposure period was measured under a microscope by taking 30 hosts randomly. However, hosts at age 9–11 d old were not measurable, and no size data for this age were obtained. The full sample of corn was then observed daily for emergence of parasitoid progeny or adult hosts.

Statistical Analyses. The larvae were arbitrarily separated by 0.14-mm intervals, except for the last larval class. The larval size in the last class ranged from 1.83 to 2.05 mm, because the overall host size range could not be divided evenly by 0.14, and because from 1.83 to 1.97 mm there were few hosts available. There were 14 host size classes including a prepupal class and a pupal class. A 2-tailed Kolmogorov-Smirnov 2-sample test was used to test differences in distributions of available hosts and parasitized hosts (Sokal and Rohlf 1981). Univariate regression analysis (SAS Institute 1988) was used to assess the relationship between larval host size (excluding the prepupae and pupae) and the following: parasitoid size, host emergence, parasitoid emergence, and percentage of parasitism. The relationship between host age and parasitoid emergence and between host age and host size was similarly analyzed. In all the regressions, median larval size or age in each class was used except for the regression evaluating the relationship between host size and parasitoid size. Lack-of-fit tests were used to evaluate model fitness where there were multiple y-variables for an x variable, and to determine if certain low r^2 values may have been primarily influenced by this dispersion of the y-values (Draper and Smith 1981).

Results

Distribution of host sizes at the time of exposure to parasitoids ranged from small larvae to pupae and was not uniform across size classes (Fig. 1A). There were decreasing host numbers with increasing host size, which is described as host number = $-1.42 + 11.08e^{(-\text{host size})}$ (equation 1; Table 1; Fig. 1A). The size of parasitized hosts ranged from small larvae with a maximum body width of 0.43 mm to prepupae (1.55 ± 0.55 mm, \pm SEM), and even 1 pupa 1.20 mm (Fig. 1D). The distributions of hosts from which female parasitoids emerged (Fig. 1B) and of hosts from which all parasitoids emerged (Fig. 1D) differed significantly (Table 2) from that for hosts available (Fig. 1A). However,

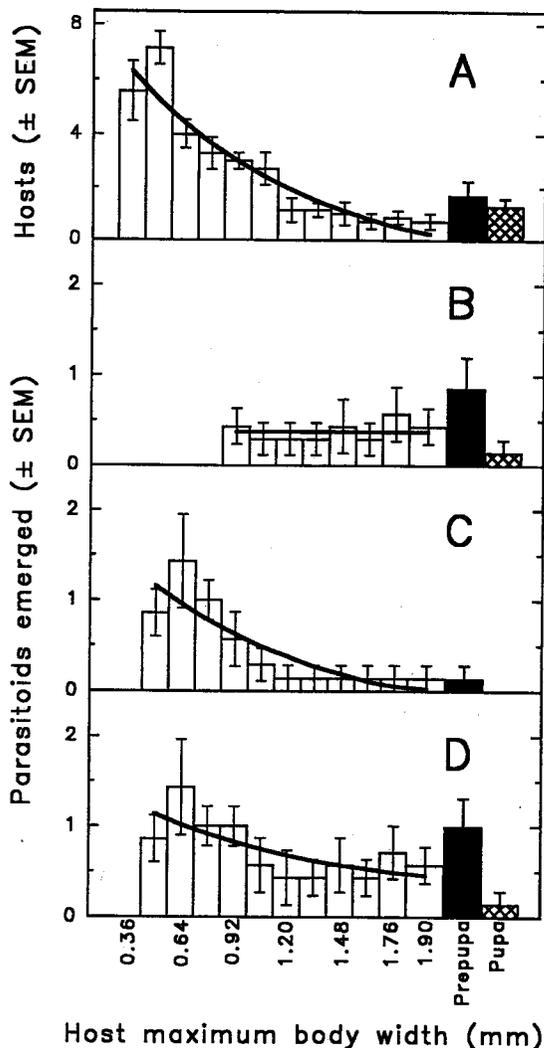


Fig. 1. Host size (maximum body width) distribution (A) and resulting parasitoid emergence, females (B), males (C), total (D). Size classes are labeled by the median value for a given range of maximum body width. Regression equations are reported in the *Results* section and descriptive statistics are shown in Tables 1 and 2.

the distribution of hosts from which male parasitoids emerged (Fig. 1C) was not significantly different (Table 2) from that of available hosts (Fig. 1A). Therefore, the distributions of hosts from which female (Fig. 1B) and male (Fig. 1C) *P. cerealellae* emerged were significantly different (Table 2). The number of female parasitoids emerging across the larval size classes that were used was constant across all host sizes and can be described by females emerged = 0.33 (equation 2; Table 1; Fig. 1B). Male parasitoid emergence decreased with increasing host size and can be described as males emerged = $-0.40 + 2.58e^{(-\text{host size})}$ (equation 3; Table 1; Fig. 1C). For total parasitoids, emer-

gence can be described as number emerged = $0.23 + 1.49e^{(-\text{host size})}$ (equation 4; Table 1; Fig. 1D). Female parasitoid progeny tended to emerge from large larvae and prepupae, whereas male parasitoid progeny tended to emerge from smaller larvae. The smallest host larvae on which a male parasitoid was produced was 0.46 mm and $\approx 64\%$ of male parasitoid progeny emerged from hosts in size classes between 0.43 and 0.85 mm wide, whereas all female parasitoid progeny emerged from hosts that were wider than 0.85 mm.

Percentage of parasitism (measured by emergence of adult parasitoids) for each host size class is shown in Fig. 2. For females emerged, percentage of parasitism yielding adult parasitoids increased with increasing host size, starting with hosts 0.78 mm wide through to a host that was 2.05 mm wide (the widest larva tested), and can be described as percentage parasitism yielding females = $9.87 + 73.58(\ln[\text{host size}])^2$ (equation 5; Table 1; Fig. 2A). For male progeny, the highest percentage of parasitism occurred on larvae between 0.57 and 0.71 mm wide, and percentage of parasitism across larval size classes is described as percentage of parasitism yielding males = $334.09 - 679.33 \ln(\text{host size})/(\text{host size}) - 315.70/(\text{Host Size})^2$ (equation 6; Table 1; Fig. 2B). For total parasitoid progeny emerged, percentage of parasitism can be described as percentage of parasitism = $26.62 + 11.17[(\text{host size})^2 \ln(\text{host size})]$ (equation 7; Table 1; Fig. 2C).

Both female and male parasitoid size were linearly correlated with host size (Fig. 3). For female parasitoid progeny, the equation is female size = $0.37 + 0.26(\text{host size})$ (equation 8; Table 1; Fig. 3). For male parasitoid progeny, the equation is male size = $0.34 + 0.23(\text{host size})$ (equation 9; Table 1; Fig. 3).

Data on parasitism success are shown in Fig. 4. Host size increased linearly with increased host age, and is described as host size = $-0.94 + 0.08(\text{host age})$ (equation 10; Table 1; Fig. 4A). There is a discrete age window for host parasitization as a function of size achieved at a given point in development. For hosts aged 9–11 or 13–15 d old, no parasitoids emerged. For hosts aged 17–19 d old, only 2.5 parasitoids emerged. Above this age, parasitoid emergence was greatly enhanced as a function of host age. Parasitoid emergence is described as parasitoids emerged = $-0.80 + 6.00 \times 10^{-3}(\text{host age})^3 - 6.69 \times 10^{-13}e^{(\text{host age})}$ (equation 11; Table 1; Fig. 4B). The number of hosts that avoided parasitism and emerged is described as a function of host age with hosts emerged = $9.75 + 119.08 \ln(\text{host age})/\text{host age}$ (equation 12; Table 1; Fig. 4C).

Discussion

In this experiment on the effect of host size distribution on a parasitoid, zero- to 1-d-old females of *S. cerealella* were used to lay eggs for 2 d. With

Table 1. Statistics for regression equations reported in the Results section and shown in Figs. 1-4

| Equation | Figure | Regression | | | | Lack-of-fit | | |
|----------|--------|------------|--------|--------|----------------|-------------|--------|-------|
| | | F | df | P | r ² | F | df | P |
| 1 | 1A | 135.25 | 1, 82 | <0.001 | 0.62 | 1.96 | 10, 72 | >0.05 |
| 2* | 1B | — | 0, 63 | — | 0.00 | 0.22 | 7, 56 | >0.1 |
| 3 | 1C | 26.11 | 1, 76 | <0.001 | 0.26 | 0.99 | 9, 66 | >0.1 |
| 4 | 1D | 6.39 | 1, 76 | <0.025 | 0.08 | 0.66 | 9, 66 | >0.1 |
| 5 | 2A | 5.24 | 1, 54 | <0.025 | 0.09 | 0.17 | 6, 48 | >0.1 |
| 6 | 2B | 3.11 | 2, 74 | <0.05 | 0.08 | 0.13 | 8, 66 | >0.1 |
| 7 | 2C | 4.58 | 1, 75 | <0.05 | 0.06 | 0.50 | 9, 66 | >0.1 |
| 8 | 3, ♀♀ | 34.46 | 1, 26 | <0.001 | 0.57 | 0.59 | 20, 26 | >0.1 |
| 9 | 3, ♂♂ | 64.28 | 1, 34 | <0.001 | 0.65 | 0.88 | 23, 34 | >0.1 |
| 10 | 4A | 569.69 | 1, 148 | <0.001 | 0.79 | 0.05 | 3, 145 | >0.01 |
| 11 | 4B | 39.77 | 2, 33 | <0.001 | 0.71 | 1.29 | 3, 30 | >0.01 |
| 12 | 4C | 35.10 | 1, 34 | <0.001 | 0.51 | 2.54 | 4, 30 | >0.05 |

*. Intercept model has no regression F value and an r² value of 0, but it is a valid model, as indicated by the lack-of-fit statistics.

12 continuous exposures to hosts at 2-d intervals, we assumed that the rate of oviposition was constant and that host size distribution would represent a uniform age distribution. However, available host numbers decreased with increasing host size. This decrease was probably caused by cumulative mortality of the host and the increased rate of growth of the late developmental stages. This curvilinearity of increasing size during development is normal for immature insects, which commonly grow most rapidly in their final instars. Thus, larvae from the 1st few time intervals were largest, with a much greater number composing the smaller size classes that represent most of the developmental period.

Pteromalus cerealellae can develop across a broad range of host sizes, from small larvae to prepupae. However, only 1 pupa was parasitized and this pupa was newly formed and in the same kernel as a parasitized prepupa. The close proximity to a detectable prepupa and vibrations caused by the body movement of the newly formed pupa may have facilitated the sole pupal parasitization. There was a threshold host size below which larvae of *S. cerealella* were not parasitized. In addition, the threshold host size for producing female parasitoid progeny was greater than that for producing male parasitoids. The tendency for female *P. cerealellae* to emerge from large hosts rather than from small ones indicates that the sex ratio of emerging *P. cerealellae* was regulated in response to host size. The regulation could result either from female control

of fertilization by laying a higher proportion of unfertilized eggs on small hosts by controlling sperm release at the time of oviposition, or possibly from differential mortality of male and female offspring during development (van Alphen and Thunnissen 1983, King 1988, Cloutier 1991). In our study it appeared more likely that differential mortality is involved. In Fig. 4B there were 2.5 ± 0.7 (mean \pm SEM) parasitoids emerged for hosts aged 17-19 d, and 27.0 ± 0.8 unparasitized hosts emerged for the same age group (Fig. 4C). For hosts aged 21-23 d, 7.0 ± 1.4 parasitoids emerged (Fig. 4B) and 25.0 ± 0.7 unparasitized hosts emerged (Fig. 4C). This indicates that the rate of parasitism is quite uniform but that the emergence of adult parasitoids was affected by the younger hosts. The size of the 17- to 19 d-old hosts was 0.55 ± 0.02 mm (Fig. 4A), which was too small to produce female parasitoids (Fig. 1B). Thus, it is likely that the initial parasitism occurs, as measured by decreased host emergence, and that the immobilized host is too small to adequately support the nutritional requirement for development of the larger female parasitoids (Fig. 3). This may explain the sex bias for our host-parasitoid system. Many researchers have reported sex-biased phenomena in other parasitic Hymenoptera (for example, Jones 1982, King 1988, Heinz and Parrella 1990, Fuester and Taylor 1991, Tillman and Cate 1993).

In solitary insect parasitoids, parasitoid size is often functionally related to host size. Our results show that the size of host *S. cerealella* affects the

Table 2. Statistics for Kolmogorov-Smirnov 2-sample tests comparing the size distribution of available hosts and the resulting enumerated distribution for emerged parasitoids for the host size classes

| Distribution | | Figures | N1 | N2 | D | P |
|-----------------|---------------|-----------|-----|----|------|---------|
| 1 | 2 | | | | | |
| Hosts available | ♀♀ emerged | 1 A and B | 239 | 28 | 0.58 | <0.0001 |
| Hosts available | Total emerged | 1 A and D | 239 | 64 | 0.28 | <0.0001 |
| Hosts available | ♂♂ emerged | 1 A and C | 239 | 36 | 0.21 | >0.05 |
| ♀♀ emerged | ♂♂ emerged | 1 B and C | 28 | 36 | 0.64 | <0.001 |

N1, sample size, distribution 1; N2, sample size, distribution 2; and D, the largest unsigned difference, Kolmogorov-Smirnov 2-sample approximate test for larger sample sizes.

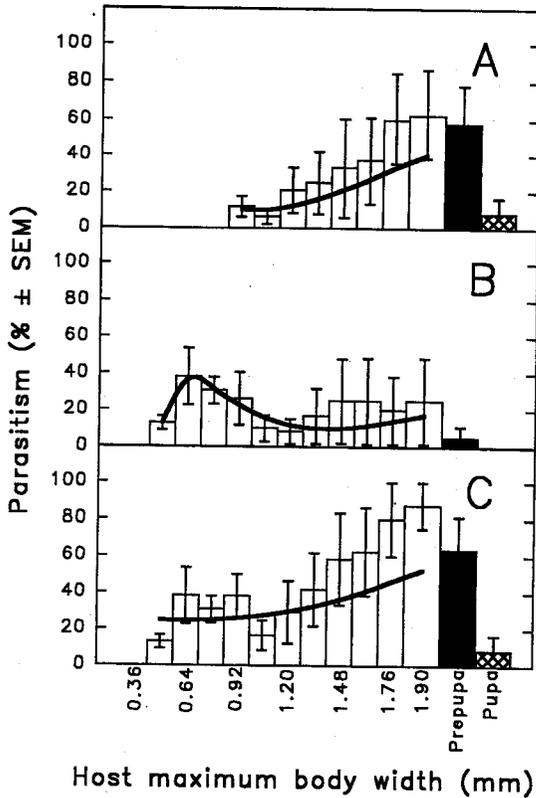


Fig. 2. Percentage of parasitism in different host size classes for female parasitoids emerging (A), male parasitoids emerging (B), and total parasitoids emerging (C). Size classes are labeled by the median value for a given range of maximum body width. Regression equations are reported in the *Results* section and descriptive statistics are shown in Table 1.

size of *P. cerealellae* offspring, and it can be concluded that larger adult parasitoids develop on larger hosts, irrespective of sex. This relationship between host size and parasitoid size has been reported for other parasitoids (for example, Sandlan 1979, Mackauer 1986, Opp and Luck 1986, Pettitt and Wietlisbach 1993). Larger female parasitoids can produce more offspring (for example, Mackauer and Kambhampati 1988, Bai et al. 1992), therefore, host size variation can affect the reproductive success of females, by influencing the survival and reproductive performance of their offspring, with possibly greater consequences for female progeny than for male (Charnov 1982).

No differences were found in numbers of parasitoids emerged at 3 host ages: 21–23, 25–27, and 29–31 d old (Fig. 4). This was probably caused by the variability in host development. Although host ages were within 2 d of one another, host size could be very different. For hosts aged 21–23, 25–27, and 29–31 d old, host size ranged from 0.54 to 1.48 mm, 0.69 to 1.73 mm, and 0.79 to 1.98 mm (including prepupae and pupae), respectively. All

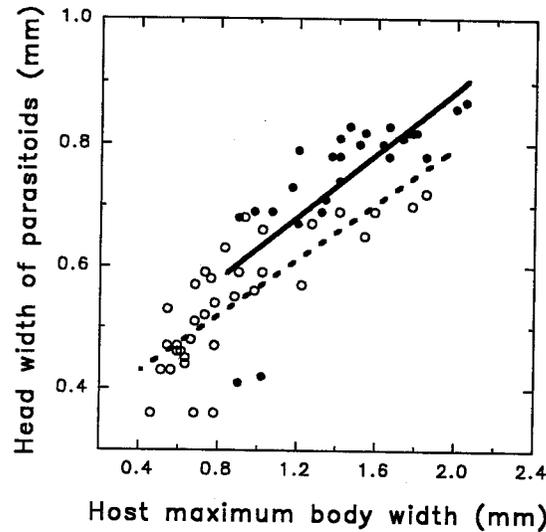


Fig. 3. Relationship between host size (maximum body width) and parasitoid size (head width). Female parasitoid (●); Male parasitoid (○). Regression equations are reported in the *Results* section and descriptive statistics are shown in Table 1.

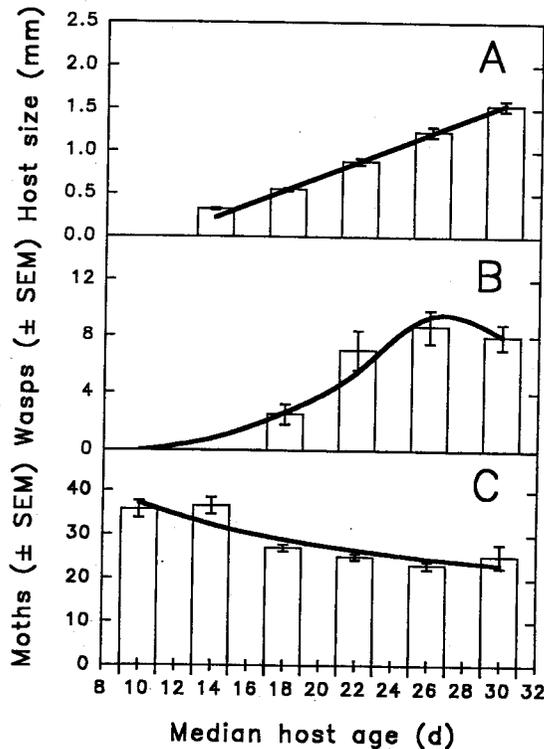


Fig. 4. Relationship between host age (median value for the age class) and host size \pm SEM distribution (A), resulting parasitoid emergence (B), and unparasitized host emergence (C). Regression equations are reported in the *Results* section and descriptive statistics are shown in Table 1.

3 age groups covered a broad range of host sizes suitable for a single female to parasitize. However, for hosts aged 17–19 d (0.34–0.84 mm), the average host size was smaller than the ideal size for producing the smaller male parasitoids and too small to support any female emergence (see Fig. 1), so very few parasitoids emerged.

In summary, we conclude that host size influences the production of male and female progeny by *P. cerealellae*, with female parasitoids emerging from larger larvae and prepupae and males emerging from smaller larvae. The size of emerging parasitoids depended on the size of the *S. cerealella* hosts on which they developed.

This information will augment decision making and release strategies for biological control of Angoumois grain moth in stored corn. An earlier study on another parasitoid system in stored corn (Smith 1993) evaluated optimal host sizes for a uniform size distribution at relatively high densities. In this study, we used low host densities and a size distribution that parallels one that would result from either a stable age distribution or from a continuous low level of infestation. The results clearly indicate that there is a very discrete host size (and time window) that allows for development of a reproducing population of this parasitoid (viable female offspring).

In stored corn, initial infestation probably occurs in the standing crop in the field and adult moths are killed by grain being moved during harvest. Therefore, a host distribution representative of recent oviposition by females (the corn is suitable for oviposition for a very short time while it is drying before harvest) is present when storage begins. This suggests that several consecutive releases over a short time, immediately after harvest, are necessary to maximize the production of parasitoid females as the host population moves through increasing (suitable) size classes. This will rapidly establish the largest possible parasitoid population for effective suppression of the developing pest population. The exact timing and frequency of releases is dependent on the environmental conditions affecting host development and can best be determined by a model for host population development. The size of the releases are best determined by a model for the parasitoid population development.

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