

Parasitism by *Pteromalus cerealellae* (Hymenoptera: Pteromalidae) on the Cowpea weevil, *Callosobruchus maculatus* (Coleoptera: Bruchidae): Host density, temperature effects, and host finding ability

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Abstract

Studies on interactions between a larval parasitoid, *Pteromalus cerealellae* (Boucek) and one of its hosts, *Callosobruchus maculatus* (F.) were carried out in the laboratory. The number of host larvae parasitized by *P. cerealellae* increased with host larvae at low densities and tended to a plateau at a density of 25 larvae per female parasitoid. Each parasitoid was able to parasitize more hosts and produced more offspring at 20 and 25 °C than at 30 °C. The number of non-infested seeds mixed with seeds infested with the last instar of *C. maculatus* did not preclude *P. cerealellae* from identifying infested seeds and attacking larvae inside them. When infested seeds were tightly packed, several host larvae escaped parasitism. *P. cerealellae* may be a useful biological control agent in newly harvested cowpea with low *C. maculatus* infestation, and lowering the temperature of the storage system may enhance the effectiveness of this parasitoid.

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1. Introduction

The cowpea weevil, *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae) is a worldwide pest of cowpea, *Vigna unguiculata* (Walp.). Infestation of cowpea by this bruchid commences in the field before mature seeds are harvested (Huignard et al., 1985). The infestation level of cowpea is very low at harvest and may sometimes be undetectable (Hagstrum, 1985; Huignard et al., 1985). *C. maculatus* multiplies very rapidly in storage where it causes very high losses (Ouedraogo et al., 1996; Sanon et al., 1998). Barring containment of the pest, complete loss of cowpea can occur within six months of storage

(Caswell, 1961). The most effective pest management tool used in the de-infestation of commercial quantities of cowpeas is fumigation with synthetic insecticides such as methyl bromide and phosphine gas (Mbata, 2004). Use and production of the fumigant methyl bromide is scheduled to end in developed countries by the year 2005 and worldwide by 2020 under the terms of the Montreal Protocol (United Nations Environment Programme, 1998). The use of phosphine in the post-harvest protection of cowpea and other dry beans has several setbacks. For instance, phosphine corrodes certain metals that form components of electrical fittings and electronics (Bond, 1984) and has the potential to cause fires and explosions (Leesch et al., 1995). Use of other pesticides in stored products is facing restriction and there is also the evolution of resistance to pesticides (Hagstrum et al., 1999; Phillips et al., 2000). Several traditional measures

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for protecting harvested cowpea are in use in subsistence agriculture but their efficacy is often unverified (Alebeek, 1996). Many species of natural enemies are associated with stored-product insects (Brower et al., 1996) and these species represent potential biological agents for these pests (Donnelly and Phillips, 2001). Some parasitoids have been investigated as biological control agents of *C. maculatus*, and they include *Uscana lariophaga* Steffan (Huis et al., 1991), *Epelmus vuiletti* (Craw) (Cortesero et al., 1993), *Lariophagus distinguendis* (Forst) (Bellows, 1985), and *Pteromalus cerealellae* (Olivier) (Brower, 1991).

Pteromalus cerealellae was formerly considered to be a monophagous parasitoid of *Sitotroga cerealellae*, but Brower (1991) found that it could parasitize other storage pests with internally developing larval stages. Brower (1991) observed that the parasitoid was highly successful in killing *C. maculatus* compared to other storage insects. Some studies on aspects of the biology of *P. cerealellae* as a parasitoid of *S. cerealellae* (Olivier) and *Sitophilus zeamais* (Motschulsky) have been investigated in the laboratory (Smith et al., 1995; Wen and Brower, 1994; Wen et al., 1995). Wen and Brower (1994) found that suppression of *S. cerealellae* increased with the release rate of the parasitoid at all host densities. Smith et al. (1995) observed *P. cerealellae* to be a more effective parasitoid of *S. cerealellae* than that of *S. zeamais*, another post-harvest pest of maize. When reared on *S. cerealellae*, the size of larvae or pre-pupae affected the sex ratio of *P. cerealellae*, and on larger host size produced more females than males (Wen et al., 1995). Currently, not much is known on the biology of *P. cerealellae* as a parasitoid of *C. maculatus*, especially with respect to the effect of host density, temperature and host spacing on the efficacy of the parasitoid.

To successfully deploy *P. cerealellae* as a biological control agent of *C. maculatus*, understanding the host parasitoid interaction is essential. The number of hosts attacked per parasitoid could be useful in predicting parasitoid development, survival and reproduction (Oaten and Murdoch, 1975). The current study in part investigated the response of *P. cerealellae* to various densities of *C. maculatus*.

Temperature is known to affect the development and survival of *Pteromalus venustus* Walker, a species related to *P. cerealellae* (Whitfield and Richards, 1985). In *P. venustus*, the range of temperatures most suitable for survival was 30–32 °C, and this coincides with temperature under which its host, leafcutter bee, *Megachile rotunda* (F.), thrives (Whitfield and Richards, 1985). Thermal adaptations in parasitoids and their hosts may vary with environments (Nealis et al., 1984), and this may affect the interaction between parasitoid and its host. In the current study, the efficacy of *P. cerealellae* as a parasitoid of cowpea weevil, its survival and production of progeny at different temperatures were investigated.

At the commencement of storage, only few seeds may harbor insect pests, and seeds may be tightly packed. It is not known if *P. cerealellae* is able to locate infested seeds from a bulk of largely non-infested seeds, or maneuver its way among tightly packed seeds to locate infested seeds. The ability of *P. cerealellae* to distinguish infested from non-infested cowpea seeds, and the effect of spacing infested seeds on host location by the parasitoid were also investigated.

2. Materials and methods

2.1. Insects—cowpea weevil and the parasitoid

Callosobruchus maculatus beetles were obtained from the Grain Marketing and Production Research Center (GMPRC), USDA-ARS, Manhattan, Kansas, and were reared on cowpea seeds (*V. unguiculata* Walp.) in 1-L wide-mouth, glass jars (about 300 beetles per jar) at 30 ± 0.5 °C, 70 ± 5% RH, and a photoperiod of 12:12 h (L:D) (Shu et al., 1996). A fresh culture was started every two weeks by placing twenty pairs (0–3 days old) of adult bruchids in 1-L jars filled up to one-fourth of its total volume with cowpea seeds, “California Black Eye” variety. The beetles were allowed 24 h to mate and lay eggs after which they were removed using an aspirator. Infested cowpea seeds were held in the 1-L jars at conditions of temperature, photoperiod and humidity specified above for 18 days. In the last larval stage, the developing larva could be seen through the thin seed coat, since the larva had eaten a portion of the cotyledon in its vicinity. The last instar of *C. maculatus* was used in rearing *P. cerealellae* and in conducting all the experiments except where otherwise indicated.

A culture of *P. cerealellae* was kindly provided by Dr. Ralph Howard, GMPRC ARS-USDA. The *P. cerealellae* colony was maintained in the laboratory by transferring about 50 adults to an 18-day-old culture of the host beetles for oviposition. Adult parasitoids were removed after five days of oviposition and the seeds bearing late instar larvae of the bruchid, assumed to bear eggs or larvae of the parasitoid, were placed individually in 10-ml glass vials with muslin lids. Emerging parasitoids were collected individually in 10-ml vials and used for the experiments. Voucher specimens of *P. cerealellae* (Number 138) have been placed at the Kansas State University Museum of Entomological and Prairie Arthropod Research, Manhattan, KS.

2.2. Response of parasitoid to host density

An experiment that evaluated the response of parasitoid to host density was conducted with cowpea weevil last instar larvae at 30 °C, 70% r.h. in petri dishes (diam-

eter 8.9 cm; volume 202.4 cm³). Three to 10 infested cowpea seeds bearing 1–5 larvae of cowpea weevil per seed were placed in petri dishes to give host densities of 3, 5, 6, 9, 10, 15, 25, and 50. At each host density, five replicates of two treatments of which one of these treatments was the control were prepared. The treatment batch was inoculated with a pair of 3-day-old male and female parasitoids per dish. Parasitoids were not introduced into the control dishes. The dishes containing the infested seeds and the parasitoids were kept for 48 h in a growth chamber maintained at 30 °C, 70% r.h. during which period the parasitoids laid eggs on the hosts. The parasitoids were all removed after 48 h and the dishes containing infested seeds and the parasitoid eggs were replaced in the growth chamber. Ten days following the removal of the parasitoids, the dishes were examined every day for the emergence of adult beetles, and subsequently from the end of second week, the dishes were inspected two times a day for emerged adult beetles and parasitoids. An earlier study has shown that *C. maculatus* developed from egg to adult in 24–30 days at 30 °C, 70% r.h., and *P. cerealellae* was observed in the laboratory to develop from egg to adult in about 3 weeks (Mbata, 1992; Mbata et al., 2004). The observation of emergence of both beetles and wasps was discontinued if a 5-day period passed without emergence of new adults. The mortality of *C. maculatus* larvae was based on the number that failed to emerge as adults. Three trials were carried out using three subsequent generations.

2.3. Effect of temperature on host parasitism and production of progeny by *P. cerealellae*

The effect of temperature on parasitism of *C. maculatus* and production of progeny by *P. cerealellae* was investigated at three temperatures, 20, 25, and 30 °C. Infested cowpea seeds bearing last instar larvae numbering between 3 and 5 were sorted for this experiment. Seven of these seeds bearing a total of 25 larvae were placed in petri dishes. At each temperature, 10 petri dishes were prepared out of which five were inoculated with a pair of 3-day-old male and female parasitoids, while parasitoids were not introduced into the remaining five, and these served as the control. The dishes containing the infested seeds and the parasitoids were kept for 48 h in a growth chamber maintained at the appropriate temperature. At the expiration of the 48 h duration the parasitoids were removed and the dishes were replaced in the chambers maintained at the above temperatures. Two weeks following the removal of the parent wasps, the dishes were inspected every day for emerged adult wasps (F1 adults) and adult bruchids until there was no emergence for five consecutive days. Mortality of host larvae exposed to wasps was based on the number of host larvae that failed to emerge as beetles.

2.4. Effect of the presence of uninfested seeds on the ability of *P. cerealellae* to locate infested seeds

Infested seeds bearing five bruchid larvae each were selected for this study. These seeds were placed five each in 40 petri dishes. Uninfested seeds numbering 0, 5, 10, 20, and 40 were added to the infested seeds in the dishes in groups of eight dishes. A pair of 3-day-old wasps (male and female) was transferred into each of the dishes. Another set of eight petri dishes containing five infested seeds bearing five bruchid larvae each was set up without wasps and this served as the control. Thereafter, the dishes were placed in a growth chamber set at 20 °C, 70% r.h. The experimental dishes had their wasps removed after 48 h, and all dishes were replaced in the growth chamber after the removal of the wasps. The experimental and control dishes were inspected for emergence of beetles and F1 wasps starting from the end of the second week following the set up of the experiments. Daily inspection was continued until no parasitoid emergence was recorded for five consecutive days.

2.5. Effect of spacing of infested seeds on the efficacy of *P. cerealellae*

This experiment investigated the ability of *P. cerealellae* to parasitize larvae in tightly packed seeds. Infested seeds numbering 25 and bearing a total of 125 larvae, with each seed having an infestation level of 4–6 larvae were placed in glass vials having volumes of 15.3, 57.4, 95.4, and 202.4 cm³ but a constant height of between 5.0 and 5.2 cm. The difference among these vials was the diameter. Eight replicates were set up for each size of container. The infested seeds in the smallest container (15.3 cm³) were tightly packed while those in the largest container (202.4 cm³) were loosely packed. A pair of 3-day-old wasps was introduced into each of the containers, and the containers were thereafter covered with muslin held in position with rubber bands. Another set of eight large containers (202.4 cm³) set up with infested seeds as described above but without wasps constituted the control. The containers were placed in a chamber maintained at 20 °C, 70% r.h. as described in the previous experiments. The wasps were removed after 48 h and the containers were replaced in the chamber and inspected for emerged adult bruchids and wasps from the end of second week of removing the parent wasps. Daily inspection was continued until no parasitoid emergence was recorded for five consecutive days. Mortality of bruchid larvae due to parasitoids was based upon the number of larvae that failed to complete development and emerge as adults.

2.6. Data analysis

In these experiments, treatment effects were determined by using analysis of variance (Proc GLM), and

LSD test ($\alpha = 0.05$) to determine significant means (SAS, 2001; Steel and Torrie, 1980). Percentage data were arcsine of square root transformed (Steel and Torrie, 1980).

3. Results

3.1. Effect of host density on parasitism

The relationship between the density of *C. maculatus* larvae and parasitism by *P. cerealellae* female is illustrated in Fig. 1. The mortality due to *P. cerealellae* at different larval host densities investigated was found to be significantly higher than natural mortality that

occurred in the control dishes (Fig. 1; $F = 710.54$, $df = 1, 269$, $P < 0.0001$). The mortalities of host bruchid larvae at different densities due to *P. cerealellae* were also significantly different ($F = 3.40$, $df = 6, 129$, $P = 0.005$). The number of larvae parasitized increased with host density up to 22 larvae per female parasitoid; beyond this density, the number of host larvae parasitized did not increase significantly.

Progeny production at different densities of host larvae is given in Fig. 2. Density of host larvae affected the number of adult progeny of the parasitoid ($F = 228.31$, $df = 6, 129$, $P = 0.0001$). Progeny production per female increased progressively with every level of host density producing significantly lower number of adult

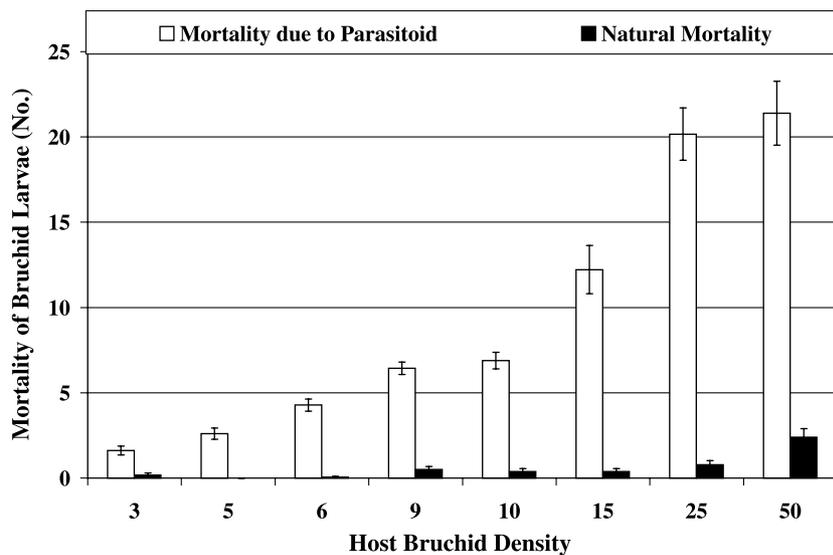


Fig. 1. Mean mortality (\pm SEM) of *C. maculatus* larvae caused by female *P. cerealellae* at different host bruchid densities at 30 °C, 70% r.h. Different upper case letters above bars indicate statistical differences ($P < 0.05$) based on LSD.

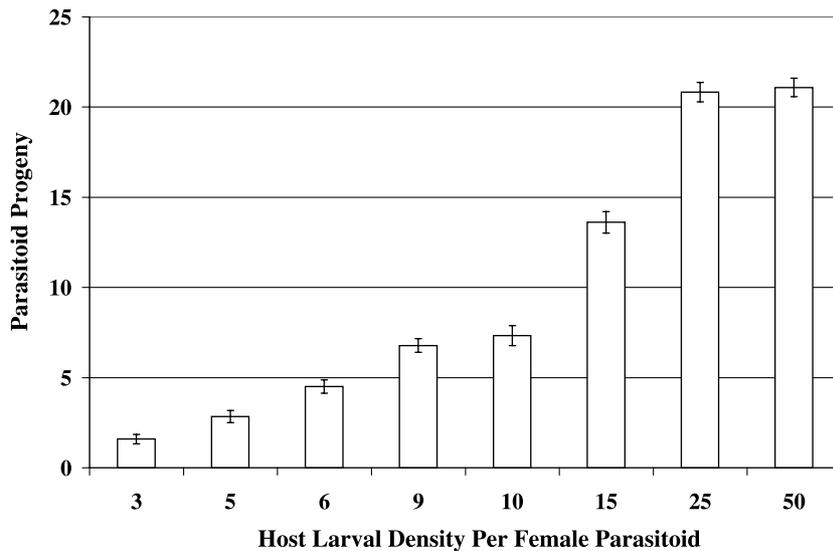


Fig. 2. Mean parasitoid F1 adults (\pm SEM) produced at different host bruchid densities at 30 °C, 70% r.h. Different upper case letters above bars indicate statistical differences ($P < 0.05$) based on LSD.

parasitoids than next higher host larval density ($P=0.05$) with the exception of host larval densities of 3 and 5; and, 25 and 50. Every host parasitized resulted in the production of one parasitoid. However, the total number of parasitoids was in some cases, a little less than the number of dead host larvae.

3.2. Effect temperature on parasitism

Temperature had a strong effect on host mortality due to the parasitoid, and this differed significantly from natural mortality in the control (Fig. 3; $F=1271.36$, $df=1, 178$, $P=0.0001$). Significantly higher mortality occurred at cooler temperatures of 20 (90.4%) and 25 °C (89.7%) than at warmer temperature of 30 °C (77.4%) ($P=0.05$).

Effect of temperature on parasitoid progeny production was significant (Fig. 4; $F=162.33$, $df=2, 87$, $P=0.0001$), and followed the same pattern as mortality.

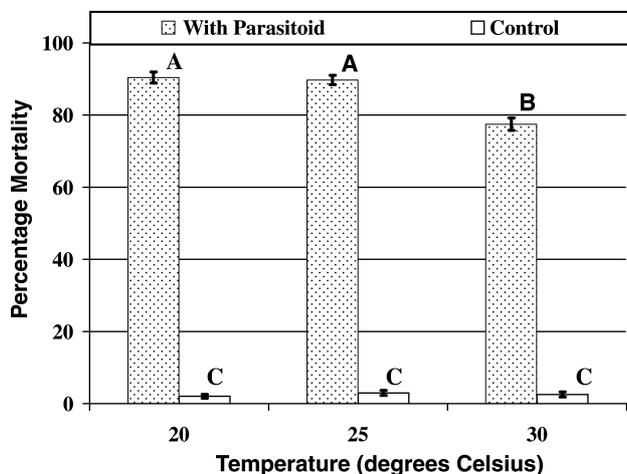


Fig. 3. Mean percentage mortality (\pm SEM) of *C. maculatus* larvae caused by a female *P. cerealellae* at different temperatures (20, 25, and 30 °C). Different upper case letters above bars indicate statistical differences ($P < 0.05$) based on LSD.

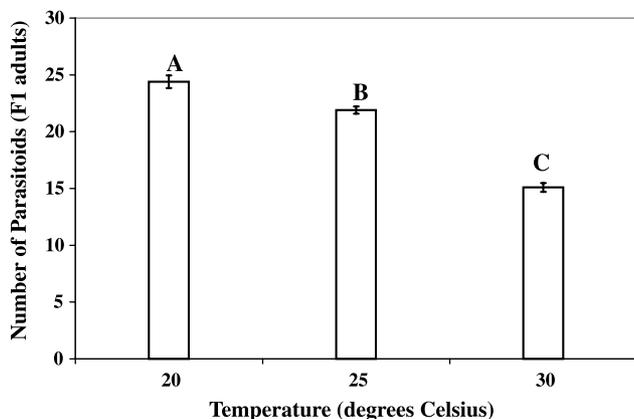


Fig. 4. Mean progeny production (\pm SEM) by *P. cerealellae* at different temperatures (20, 25, and 30 °C). Different upper case letters above bars indicate statistical differences ($P < 0.05$) based on LSD.

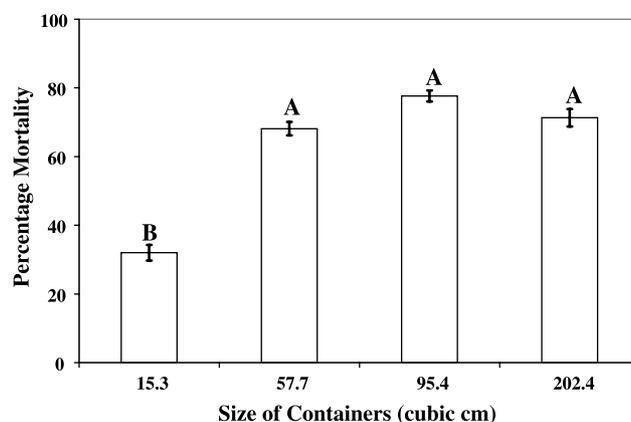


Fig. 5. Mean percentage mortality (\pm SEM) of *C. maculatus* larvae caused by a female *P. cerealellae* when the same number of infested seeds bearing the same number of *C. maculatus* larvae was placed in containers of different sizes. Different upper case letters above bars indicate statistical differences ($P < 0.05$) based on LSD.

The number of parasitoid adults that emerged was highest (24.4) at 20 °C and lowest (15.09) at 30 °C. The numbers of adult parasitoids that emerged at different temperatures were significantly different ($P=0.05$).

3.3. Effect of presence of uninfested seeds on the ability of parasitoid to locate host in infested seeds

The percentage mortalities at different densities of non-infested seeds were not significantly different from each other, and ranged between 88.0 and 92.5%, but all were significantly different from the control mortality that was 3.0% ($F=110.61$, $df=5, 42$; $P < 0.0001$), which is the natural mortality. The parasitoids were able to locate infested seeds among non-infested ones.

3.4. Effect of spacing of infested seeds on the efficacy of *P. cerealellae*

The effect of container size on the efficacy of the parasitoid is shown in Fig. 5. Analysis of variance showed that the size of containers had a significant effect on the mortality of cowpea weevil larvae ascribed to *P. cerealellae* ($F=187.66$, $df=4, 35$, $P < 0.0001$). Mortality caused by the parasitoid did not differ significantly in vials with sizes 202.4, 95.4, and 57.4 cm³, but mortality recorded in the smallest vials of 15.4 cm³ was significantly lower than those in larger vials.

4. Discussion

The number of larvae parasitized increased with host density up to 22 larvae per female parasitoid; beyond this density, the number of host larvae parasitized did not increase significantly. Increases in parasitism by parasitoids with increase in host numbers have been

observed in several parasitoids (Alebeek et al., 1996; Donnelly and Phillips, 2001). Given the exposure time (48 h) of the parasitoid to the hosts, the time available for the parasitoid to deposit eggs on host may not be the most important limiting factor, rather initial egg load and egg maturation by the female parasitoid may play an important role in the rate of parasitism of the host larvae (Heimpel and Rosenheim, 1998). Alebeek et al. (1996) observed the limiting effect of parasitoid's initial egg load and maturation on the rate of parasitism in the egg-parasitoid, *U. lariophaga*. From the density of 22 host larvae and upwards per female parasitoid, the mean number of bruchid larvae that can be parasitized ranged from 19 to 21 within 48 h at 30 °C, that is the rate of 9.5–10.5 eggs per day. In a related Pteromalidae, *Lariophagus distinguendus*, an oviposition rate of 7.9 eggs per day was observed for the first six days (Bellows, 1985). All parasitoid species can be classified as either proovigenic species, in which the number of eggs stored in the ovaries equals the maximum potential lifetime fecundity, or synovigenic species in which reproductive potential can exceed the capacity to store eggs (Heimpel and Rosenheim, 1998; Jervis et al., 2001; Jervis and Kidd, 1986). The present results suggest that *P. cerealellae* will most likely qualify as a synovigenic species since time available for oviposition was not a limiting factor on the rate of parasitism. One possible implication of *P. cerealellae* being a synovigenic species is that it is a long living species (Jervis et al., 2001). Thus, upon emergence as adult, *P. cerealellae* can parasitize fully grown bruchid larvae and wait for young larvae to attain last instar. Additional work is needed to validate the present classification of *P. cerealellae* as a synovigenic species, as this could be useful in the application of biological control using this parasitoid in a conservation strategy to manage infestation of harvested cowpea by the cowpea weevils.

Pteromalus cerealellae was found to produce more progeny and was a more effective parasitoid of cowpea weevil larvae at low temperatures of 20 and 25 °C than at high temperature of 30 °C. However, in a related species, *P. venustus*, a parasitoid of the alfalfa leafcutter bee, *M. rotunda* (F.), the rate of egg development was found to increase with temperature from 26 to 32 °C while that of larval and pupal development increased with temperature from 20 to 36 °C, beyond 36 °C, there was a decrease in the rate of development of all the stages (Whitfield and Richards, 1985). While reasonable increases in temperature can accelerate insect development, increases in temperature that shorten the durations of the late larval and the pre-pupal stages will increase the chances of the host escaping parasitism in the *P. cerealellae*–cowpea weevil system. Low temperatures of 20 and 25 °C slowed down the development of the cowpea weevil's larvae or pre-pupae to pupae, allowing the parasitoid more time to parasitize the developing weevil. Suppression of hosts and attack rates by parasitoids in stored-product

systems have been observed to be enhanced at lower temperatures compared to higher ones. For instance, Toews et al. (2001) observed that *Theocolax elegans* (Westwood), a Pteromalid parasitoid of *Rhyzopertha dominica* (F.) suppressed the host better at low temperature (27 °C) than at high temperature (34 °C). The attack rate by *Cephalonomia waterstoni* (Gahan) (Hymenoptera: Bethyilidae) on the lesser grain beetle, *Cryptolestes ferrugineus* (Stephens) was two and one-half times greater at 25 °C than at 38 °C (Flinn, 1991). Likewise, lower temperature compared to a higher one improved the effectiveness of *T. elegans* in suppressing the lesser grain beetle (Flinn, 1998; Flinn et al., 1996). Deployment of *P. cerealellae* in a cowpea storage system maintained at a temperature range of 20–25 °C would enhance both parasitism of bruchid larvae and progeny production by the parasitoid.

Pteromalus cerealellae females were able to distinguish infested cowpea seeds from non-infested seeds since increases in the number of non-infested seeds did not lower the number of bruchid larvae parasitized. Some odor sources such as bruchid sex pheromone, oviposition marker pheromone, and infested seeds have been observed to generate positive olfactometry response (Mbata et al., 2004). However, no information is available on how this parasitoid can differentiate at a close range, seeds bearing internally developing seed beetles from non-infested seeds. It is probable that ultrasonic vibrations generated by the internally developing larvae (Shade et al., 1990) may be used in detecting larvae-bearing seeds. Behavioral studies are needed to fully understand how the parasitoid is able to distinguish infested from non-infested seeds, and parasitized from non-parasitized larvae. When infested seeds were tightly packed, a drop in the number of parasitized larvae was observed. This is likely due to the inability of the parasitoid to maneuver among seeds. *P. cerealellae* has the potential for biological control of *C. maculatus* in cowpea storage systems infested with low levels of the bruchid and maintained at low temperature range of 20–25 °C.

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