



Longevity, fecundity, and progeny sex ratio of *Pteromalus cerealellae* in relation to diet, host provision, and mating

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Abstract

We investigated the effects of diet (sugar feeding), host provision, and mating on the longevity, fecundity, and progeny sex ratio of *Pteromalus cerealellae* (Ashmead) (Hymenoptera: Pteromalidae), an ectoparasitoid of several stored-product insects. Sugar feeding (25% sucrose solution) increased male lifespan by a factor of 3–4 relative to sugar-starved (provided water only) or completely starved (provided no water and no sugar solution) males, irrespective of mating status or host provision. Sugar feeding also increased longevity of females which were not provided hosts, but had no effect on longevity of females which were provided hosts, suggesting that supplemental sugar feeding is beneficial to females only in the absence of hosts. Females had a significantly greater longevity than males: Mean (\pm SE) longevity of sugar-fed unmated females provisioned with no hosts (36.3 ± 1.2 days) was significantly greater than mean longevity of sugar-fed unmated males provisioned with no hosts (29.7 ± 0.9 days). A negative effect of mating on longevity was recorded only in the absence of hosts but not when hosts were provided. In general, sugar feeding resulted in a modest increase in progeny production by female *P. cerealellae* and this was significant for one batch of attacked hosts. However, cumulative lifetime progeny (mean \pm SE) of sugar-fed females (64.2 ± 9.2) was not significantly greater than that of sugar-starved (44.5 ± 6.8), or completely starved (54.5 ± 9.3) females. Nevertheless, progeny of sugar-fed females was female-biased (53% females) compared to male-biased progeny recorded for completely-starved females (37% females). These results suggest the potential impact of sugar feeding on survival, fecundity, and sex allocation in *P. cerealellae*.

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1. Introduction

Parasitoids play a major role in sustainable agriculture through their ability to regulate populations of herbivorous insect pests. Many species of parasitoids are associated with stored-product insects with potential for utilization as biological control agents (Brower et al., 1996). One of such parasitoid species is *Pteromalus cerealellae* (Ashmead) (Hymenoptera: Pteromalidae), an ectoparasitoid of several pests of stored grains (Brower, 1991) including the cowpea bruchid, *Callosobruchus maculatus* (Fabricius) (Coleoptera:

Chrysomelidae) (Brower, 1991; Mbata et al., 2005). The ongoing interest in the potential utilization of *P. cerealellae* for biological control of stored product insects (Brower, 1991; Mbata et al., 2005) is, however, hindered by a gross lack of information on several aspects of its biology and life history strategy. For example, little is known about the effects of food provision and physiological factors such as age and mating on survival and fitness of *P. cerealellae*.

Although a variety of factors may be responsible for the shortened longevity of parasitoids in the field compared with laboratory populations, poor diet may play a significant role. Several parasitoids, in particular females, are known to utilize host and non-host foods (e.g., sugar sources) with important ramifications on their reproductive

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success (Jervis et al., 1996). Host feeding (consumption of host tissue) is a common occurrence in female parasitoids and has been observed in over 140 species across 17 families of Hymenoptera (Jervis and Kidd, 1986) and Diptera (Nettles, 1987). In addition to host feeding, several parasitoids have also been reported to feed on artificial (e.g., sucrose solution and honey) and naturally-occurring (e.g., nectar and homopteran honeydew) sugar sources both in the laboratory and field (Jervis et al., 1993; Heimpel et al., 1997; Olson et al., 2000; Fadamiro and Heimpel, 2001; Lee et al., 2004; Fadamiro and Chen, 2005; Fadamiro et al., 2005). Sugar feeding has been demonstrated to increase the survival of adult parasitoids (Jervis et al., 1996; Leatemia et al., 1995; Wäckers, 2001; Fadamiro and Chen, 2005; Fadamiro et al., 2005), and may enhance fecundity, either through a positive effect on the rate of egg maturation or through an increased lifespan, or both (Schmale et al., 2001; Heimpel and Jervis, 2005). However, some studies have suggested that host feeding may be a superior source of nutrients for parasitoid survival and fecundity than sugar feeding (Jervis and Kidd, 1986; Van Lenteren et al., 1987; Heimpel and Collier, 1996). In contrast, provision of hosts may have a negative impact on parasitoid longevity possibly by allowing for oviposition which may result in the death of females (Lim, 1986). No previous information is available on the ability of *P. cerealellae* to feed either on the hemolymph or the body tissues of its hosts.

Mating is another factor that can potentially impact insect survival. Mating can serve to increase allocation of resources to reproductive tasks such as oogenesis and egg maturation in females leading to a significant reduction in lifespan (Partridge and Farquhar, 1981; Reznick, 1985; Ellers, 1996; Wheeler, 1996; Jacob and Evans, 2000). In fact, several studies have reported a negative impact of mating on longevity of parasitoids (Li et al., 1993; Carpenter, 1995; Jacob and Evans, 2000; Sagarra et al., 2002). In this study, we investigated the effects of diet, host provision, mating, and possible interactions of these factors on the longevity and fecundity of *P. cerealellae*. Knowledge of the influence of these factors on the fitness of *P. cerealellae* should aid in the current efforts aimed at utilizing this parasitoid for biological control of stored-product insects.

2. Materials and methods

2.1. Insects

Callosobruchus maculatus was utilized as host for *P. cerealellae* in this study. The starting culture of *C. maculatus* was initially obtained from Fort Valley State University, Fort Valley, GA, USA (contact: Dr. George Mbata), where it has been reared continuously on cowpea seeds (*Vigna unguiculata* Walp.) for several years. *Callosobruchus maculatus* was reared in our laboratory on cowpea seeds (California Black Eyed variety) in 1-liter wide-mouthed Mason glass jars. A fresh culture was started

every five days by placing ~25 pairs of 3-day-old mated *C. maculatus* in a glass jar containing ~100 g of cowpea seeds held at $30 \pm 1^\circ\text{C}$, $70 \pm 5\%$ r.h., and L12: D12 (Mbata et al., 2005). The beetles were allowed to lay eggs on the seeds for 24 h after which they were removed with an aspirator. The infested seeds were incubated at the conditions specified above for 15–18 days (Mbata et al., 2005). Based on the results of a preliminary experiment (unpublished data), fourth instar larvae of *C. maculatus* were used as parasitoid hosts for *P. cerealellae* in this study.

The original culture of *P. cerealellae* was obtained from Fort Valley State University, Fort Valley, GA, USA where the parasitoid has been reared continuously for several years. *Pteromalus cerealellae* culture was maintained in our laboratory by transferring about 30 adult pairs onto a glass jar containing *C. maculatus*-infested cowpea seeds at a stage when most of the bruchid larvae were at the fourth larval instar. This was determined in a preliminary experiment to occur approximately 15 days after infestation of cowpea seeds under our rearing conditions. The jars were held at the environmental conditions stated above for *C. maculatus*. Adult *P. cerealellae* were removed from the jars after five days of oviposition and the attacked *C. maculatus* larvae incubated in a growth chamber at the above environmental conditions until the emergence of adult parasitoids.

2.2. Effect of diet, host provision, and mating on longevity

This experiment simultaneously tested the effects and interactions of diet (3 diet treatments), host provision (host provisioned versus no host), and mating (unmated versus mated) on longevity of female and male *P. cerealellae*. The three diet treatments evaluated were: (i) completely starved (provided no water and no sugar), (ii) sugar-starved (provided water only), and (iii) sugar-fed. The various combinations of the three factors (diet, host feeding, and mating) resulted in a total of 12 treatment combinations for each sex. We demonstrated in a preliminary experiment that *P. cerealellae* is arrhenotokous. Female progeny is produced only when parent female has mated. Freshly emerged adults of *P. cerealellae* were placed in groups of two individuals either of the same sex (unmated treatments) or of opposite sex (mated treatments) in a 6-cm diameter plastic Petri dish containing either 10 uninfested cowpea seeds (no host treatments) or infested cowpea seeds containing ~80 fourth instar larvae of *C. maculatus* (host provisioned treatments). Petri dishes were then randomly assigned to the three diet treatments (completely starved, sugar-starved, or sugar-fed). With the exception of the completely starved treatment, water was provided in all treatments by filling a 0.5 mL microcentrifuge tube with distilled water and threading a cotton string through a hole in the cap of the tube. Water tubes were refilled as needed. For the treatments involving sugar feeding, 25% sucrose solution was smeared on the inside of the Petri dish cover as needed (every other day). In the treatments involving

host provision, parasitoids were supplied with fresh hosts (~80 fourth instar larvae of *C. maculatus*) every 5 days. The number of hosts was determined by counting the number of egg plugs of *C. maculatus* on infested cowpea seeds. Only seeds with 1–3 *C. maculatus* egg plugs were used. In this and subsequent experiments, Petri dishes were kept at $30 \pm 1^\circ\text{C}$, $70 \pm 5\%$ r.h., and L12:D12. Petri dishes were checked daily for parasitoid mortality. Twenty parasitoids of each sex were tested for each treatment combination. Data were analyzed by using proportional hazard modeling (SAS Institute, 1998) to test for effects and interactions of diet, host provision, mating, and sex on survivorship. Longevity data for each sex were then square-root ($\sqrt{(x + 0.5)}$) transformed and subjected to analysis of variance (ANOVA) followed by the Tukey–Kramer honestly significant difference (HSD) test for multiple comparisons of means at $P < 0.05$ (JMPIN Version 5.1, SAS Institute, 1998).

2.3. Effect of diet on progeny production

This experiment was conducted to determine lifetime progeny production (lifetime fecundity) by *P. cerealellae* females provided different diet treatments. Following the test protocols described in the previous experiment, freshly-emerged females were paired each with a male (for mating) in a 6-cm diameter plastic Petri dish. Infested cowpea seeds containing ~80 fourth instar larvae of *C. maculatus* were provided in each Petri dish as hosts for females to oviposit on. The females were then assigned to each of the three diet treatments evaluated in Experiment 1 (completely starved, sugar-starved, or sugar-fed). In order to maximize opportunity for oviposition, females were provisioned with new hosts in batches every 5 days throughout their lifetime. Provision of new batches of hosts to females every 5 days (i.e., at ages 1, 6, 11, 16, and 21 days) made it possible to determine any temporal fluctuations in oviposition and the timing (age) of peak oviposition. Based on data from Experiment 1 which showed an average longevity of about 25 days for female *P. cerealellae*, this experiment was continued until females were 25 days old thereby allowing each female to oviposit on 5 successive batches of new hosts (batch 1 = progeny produced at ages 1–5 days, batch 2 = progeny produced at ages 6–10 days, batch 3 = progeny produced at ages 11–15 days, batch 4 = progeny produced at ages 16–20 days, batch 5 = progeny produced at ages 21–25 days). Each batch of attacked host was incubated separately in a growth chamber until emergence of adult parasitoids. Emerging parasitoids from each batch were sexed and counted to determine progeny production and offspring sex ratio. For each female, the sum of number of progeny produced from successive batches of attacked hosts (5 batches total) was used to calculate cumulative (total) lifetime progeny production. At least 21 females were tested per diet treatment. Progeny production data obtained at each age were square-root transformed ($\sqrt{(x + 0.5)}$) and analyzed by using two-way

factorial ANOVA followed by the Tukey–Kramer HSD test for multiple comparisons of means at ($P < 0.05$) to test for effects of diet, age, and interactions on progeny production. Cumulative fecundity data were further analyzed by using one-way ANOVA followed by the Tukey–Kramer HSD test ($P < 0.05$). Data on offspring sex ratio were analyzed by using a χ^2 2×2 test of independence with Yales correction for continuity (Parker, 1979) to test for significant deviation ($P < 0.05$) from an expected 1:1 sex ratio of the progeny recorded per diet treatment for each host batch, as well as for the cumulative progeny.

3. Results

3.1. Effects of diet, host provision, and mating on longevity

Proportional hazard analysis showed significant effects of diet ($\chi^2 = 471.03$, $df = 2$, $P < 0.0001$), host provision ($\chi^2 = 21.25$, $df = 1$, $P < 0.0001$), sex ($\chi^2 = 291.52$, $df = 1$, $P < 0.0001$), and mating ($\chi^2 = 12.36$, $df = 1$, $P < 0.0001$) on the longevity of *P. cerealellae* (Table 1). In addition, significant interactions were recorded between mating and host provision ($\chi^2 = 17.70$, $df = 1$, $P < 0.0001$), diet and host provision ($\chi^2 = 49.67$, $df = 1$, $P < 0.0001$), diet and sex ($\chi^2 = 141.49$, $df = 2$, $P < 0.0001$), as well as a significant diet \times host provision \times sex interaction ($\chi^2 = 43.97$, $df = 2$, $P < 0.0001$), suggesting that longevity is also influenced by multiple interactions among the various factors.

Differences were recorded on the influence of sugar feeding (diet) and host provision on longevity of mated and unmated female *P. cerealellae*. For females, sugar feeding exerted a significant positive effect on longevity when no hosts were provided, but no significant effect of sugar feeding was recorded when females were provisioned with hosts (Fig. 1), possibly suggesting that females are capable of utilizing host materials for optimum longevity. Sugar feeding also exerted a significant effect on longevity of unmated females, irrespective of whether or not they were

Table 1
Proportional hazard model testing for effects of diet, host provision, sex, and interactions of these variables on longevity of *P. cerealellae*

Source of variation	df	χ^2	P
Diet	2	471.03	<0.0001
Host provision	1	21.25	<0.0001
Sex	1	291.52	<0.0001
Mating	1	12.36	0.0004
Diet \times host	2	49.67	<0.0001
Diet \times sex	2	141.49	<0.0001
Diet \times mating	2	3.70	0.16
Host \times sex	1	0.49	0.48
Host \times mating	1	17.70	<0.0001
Sex \times mating	1	0.41	0.52
Diet \times host \times sex	2	43.97	<0.0001
Diet \times sex \times mating	2	0.15	0.93
Host \times sex \times mating	1	1.17	0.28
Diet \times host \times mating	2	3.01	0.22
Mating \times diet \times host \times sex	2	0.80	0.67

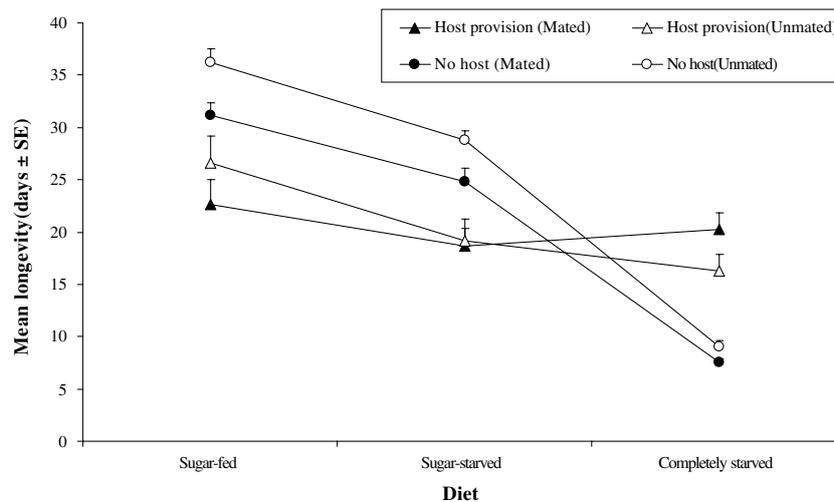


Fig. 1. Effects of diet and host provision on longevity of female *P. cerealellae*. Figure shows the influence of diet (sugar-fed, sugar-starved, and completely starved) on mean longevity (days \pm SE) of mated and unmated females in the presence or absence of hosts.

provisioned with hosts (Fig. 1). Similarly, sugar feeding exerted a significant effect on male survival: longevity of sugar-fed males was 3–4 times greater than longevity of sugar-starved or completely-starved males, irrespective of their mating status and whether or not they were provisioned with hosts (Fig. 2). Provision of hosts had a positive effect on longevity of mated males, but had no effect on longevity of unmated males, suggesting that male *P. cerealellae* are incapable of initiating host feeding, but may obtain valuable host materials from punctures made by the females. The effect of mating on male longevity was dependent upon whether or not hosts were provided. A negative impact of mating on longevity was recorded for males provided no hosts: Unmated males provisioned with no hosts had a greater longevity than mated males provisioned with no hosts, irrespective of diet treatment (Fig. 2). However, com-

pletely-starved mated males which were provided hosts had a greater longevity than completely-starved unmated males, further confirming that males paired with females provisioned with hosts could obtain host resources from punctures made by females which could result in increase in male lifespan. In addition, while a negative effect of mating was recorded on longevity of sugar-fed males provisioned with no hosts, no significant effect of mating on longevity was recorded for sugar-fed males provisioned with hosts, suggesting that provision of hosts may lessen the potential negative impact of mating on male longevity. In general, longevity was greater for females than for males, irrespective of the treatment combination. For instance, average longevity of completely-starved unmated female and male *P. cerealellae* provisioned with no hosts was 9.00 ± 0.58 and 5.70 ± 0.25 , respectively (Figs. 1 and 2).

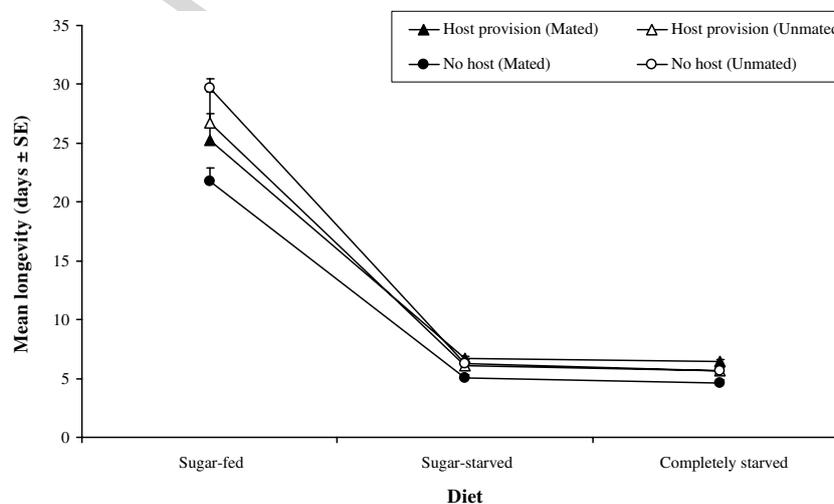


Fig. 2. Effects of diet and host provision on longevity of male *P. cerealellae*. Figure shows the influence of diet (sugar-fed, sugar-starved, and completely starved) on mean longevity (days \pm SE) of mated and unmated males in the presence or absence of hosts.

3.2. Effect of diet on progeny production

Two-way factorial ANOVA showed no significant effects of diet ($F = 31.83$, $df = 2$, $P = 0.16$) and age (batch) ($F = 54.24$, $df = 4$, $P < 0.0001$) on progeny production by female *P. cerealellae*. Progeny production by sugar-fed females on batch 4 hosts (i.e., progeny produced by females at ages 16–20 days) was significantly greater than progeny production by completely starved females at the same age range ($F = 3.37$, $df = 2$, $P = 0.04$, Fig. 3). Although, a similar trend showing numerically greater progeny production by sugar-fed females was recorded for the other batches of hosts (i.e., batches 1, 2, 3, and 5), this was not significant (Fig. 3). In general, age (batch) had a significant effect on progeny production, irrespective of diet: greater progeny was produced earlier in life than later in life (Fig. 3). Mean (\pm SE) progeny production by sugar-fed females was significantly greater at ages 1–5 days (37.86 ± 5.93) than at ages 6–10 days (16.67 ± 3.95), or at subsequent age ranges. Approximately, 60–70% of the total lifetime progeny were produced within the first 5 days of female life, suggesting early peak oviposition (Fig. 3). The lowest number of progeny was produced on the last batch of attacked hosts (at ages 21–25 days). Similar results were obtained for sugar-starved and completely starved females, suggesting that diet has no effect on the timing of peak oviposition.

Mean cumulative (total) lifetime progeny production (lifetime fecundity) was not significantly different among diet treatments ($F = 1.15$, $df = 2$, $P = 0.32$). Mean (\pm SE) lifetime fecundity (total/cumulative progeny) of sugar-fed females (64.24 ± 9.16) was not significantly greater than lifetime fecundity of sugar-starved (44.50 ± 6.81) or completely starved (54.55 ± 9.26) females. Nevertheless, signif-

icant effects of diet and age were recorded on sex ratio of progeny. In general, the progeny produced during the first 5 days of female life (at ages 1–5 days) was female-biased, compared to male-biased progeny recorded later in life (Fig. 4). Further chi-square analysis of the lifetime fecundity data showed a significant female-biased offspring for sugar-fed females (53%) compared to the significant male-biased offspring recorded for completely starved (37%) females. However, no significant difference in sex ratio was recorded for females provided water only (sugar-starved) (Fig. 4).

4. Discussion

Sugar feeding is a major factor influencing adult lifespan of female and male *P. cerealellae*. Sugar feeding increased male lifespan by a factor of 3–4 relative to sugar-starved or completely starved males, irrespective of mating status or host provision. However, the magnitude of the impact of sugar feeding on longevity of females is affected by mating status and host provision. Our results suggest the following among others: (i) females are capable of obtaining resources from host feeding for optimal longevity, (ii) sugar feeding represents an alternative food source for females in achieving optimum longevity, (iii) mating could have a negative impact on longevity of females and males *P. cerealellae* irrespective of whether or not there are opportunities for host feeding, (iv) males are incapable of initiating host feeding, and sugar feeding therefore represents a major food source available for males to achieve optimum longevity, and (v) males paired with females provisioned with hosts (mated treatments) could benefit from host feeding by obtaining resources from hosts punctured by females.

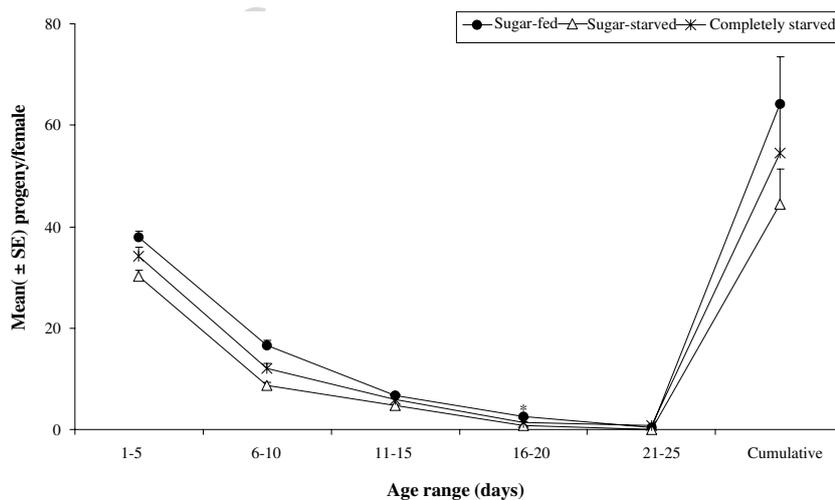


Fig. 3. Fecundity of female *P. cerealellae* of different age ranges provisioned with different diet treatments. Figure shows mean (\pm SE) number of progeny produced per female at different age ranges, and the total cumulative progeny (lifetime fecundity). In this and the next figure, females were provisioned with new hosts (infested cowpea seeds containing ~ 80 fourth instar larvae of *C. maculatus*) in batches every 5 days (i.e., at ages 1, 6, 11, 16, and 21 days) throughout their lifetime (~ 25 days) thereby allowing each female to oviposit on 5 successive batches of new hosts (batch 1 = progeny produced at ages 1–5 days, batch 2 = progeny produced at ages 6–10 days, batch 3 = progeny produced at ages 11–15, batch 4 = progeny produced at ages 16–20 days, batch 5 = progeny produced at ages 21–25 days). Means for the same age range and for cumulative progeny followed by different letters are significant ($P < 0.05$, Tukey HSD test).

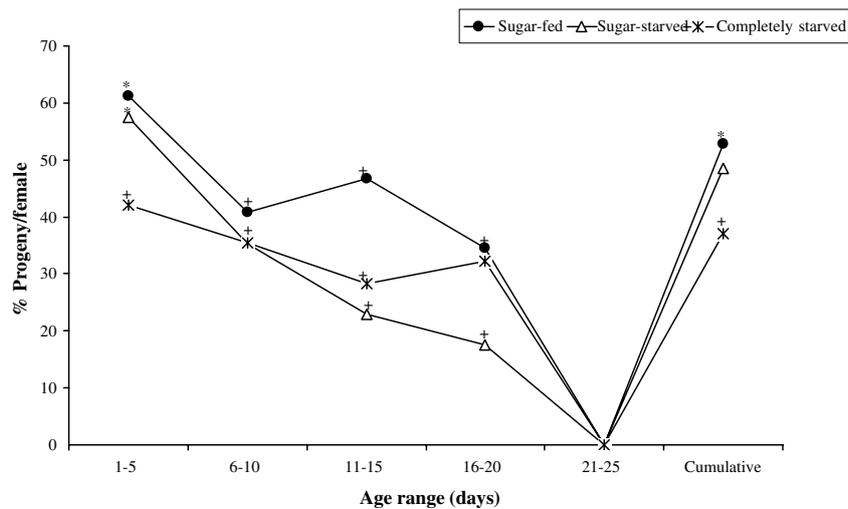


Fig. 4. Sex ratio of offspring produced by female *P. cerealellae* of different age ranges provisioned with different diet treatments. Figure shows proportion (percent) of female progeny *, significant female-biased progeny; +, significant male-biased progeny ($P < 0.05$, χ^2 2×2 analysis).

The positive impact of sugar feeding on adult longevity has been demonstrated for several parasitoids species from different taxa (Heimpel et al., 1997; Olson et al., 2000; Fadamiro and Heimpel, 2001; Lee et al., 2004; Fadamiro and Chen, 2005; Fadamiro et al., 2005; Chen et al., 2005). For some of these species, provision of water was also shown to increase longevity compared to completely starved (no water, no sugar) adults (Fadamiro et al., 2005; Chen et al., 2005). However, no difference in longevity was recorded between water-provided (sugar-starved) and completely starved male and female *P. cerealellae* provisioned with hosts in the current study, suggesting the positive effect of host availability on longevity of starved adults, as reported for *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) (Leatemia et al., 1995). In general, average lifespan was greater for female than for male *P. cerealellae*, as has been reported for several hymenopteran parasitoids (Olson et al., 2000; Fadamiro and Heimpel, 2001).

Our longevity data showed that only females that were not provided hosts benefited significantly from sugar feeding: Sugar feeding did not result in significant increase in the lifespan of females provisioned with hosts. These results suggest that female *P. cerealellae* are capable of obtaining resources from host feeding for optimal longevity, and that supplemental sugar feeding is beneficial only in the absence of hosts. Host feeding, a widespread phenomenon in female parasitoids (Jervis and Kidd, 1986; Nettles, 1987), has been shown to increase adult longevity, particularly in the absence of non-host food (Narayanan and Mookherjee, 1955), similar to the results of the current study. In addition, we recorded higher longevity for males paired with females (mated males) provisioned with hosts compared to unpaired males (unmated males) provisioned with hosts suggesting that male *P. cerealellae* are capable of obtaining host materials from punctures made by the females for enhanced survival. Provision of hosts may adversely impact longevity possibly by allowing for oviposition which may result in the death of females (Lim, 1986).

Similar adverse effect of host availability on lifespan was obtained for *P. cerealellae* in the present study.

In general, mating had a negative effect on longevity of female and male *P. cerealellae* in the absence of hosts, but not when hosts were provided. A trade-off between mating and longevity has been reported for several parasitoids (Li et al., 1993; Carpenter, 1995; Jacob and Evans, 2000; Sagarra et al., 2002). A common hypothesis is that mating can negatively impact longevity by stimulating allocation of resources to reproductive activities (e.g., oogenesis and egg maturation in females), thereby reducing resources available for other life processes (Partridge and Farquhar, 1981; Reznick, 1985; Eilers, 1996; Jacob and Evans, 2000). This potential trade-off between mating and longevity is more likely to occur when energy resources are limited, or in the absence of a high quality food, as demonstrated by Jacob and Evans (2000). The authors reported adverse impact of mating on longevity of *Bathyplectes curculionis* (Thomson) (Hymenoptera: Ichneumonidae) females only in the absence of a high quality food source such as honey (Jacob and Evans, 2000).

In the second experiment, we compared lifetime progeny production (lifetime fecundity) of females provided different diet treatments; each female having been supplied with a fresh batch of hosts every 5 days throughout her lifetime. Data from this experiment showed a major effect of age on progeny production with the greatest number of progeny (>60% of total progeny produced per female) produced during the first five days of life, irrespective of diet treatment, suggesting that peak oviposition by female *P. cerealellae* occurs early in life. In general, sugar feeding had a modest effect on the number of progeny produced on each successive batch of hosts: a significant effect of sugar feeding was recorded only for progeny produced by females at ages 16–20 days (batch 4 hosts). Nevertheless, cumulative total lifetime progeny was not significantly different among diet treatments. However, the higher female progeny recorded for sugar-fed females compared to completely starved females may indicate a potential benefit of sugar

feeding in the production of female-biased progeny, an important consideration in the utilization of biological control agents. Sex allocation in many parasitoid species is known to be influenced by host quality (Chow and Heinz, 2005). Our results suggest that diet quality may also have an effect on sex allocation, as was reported by Leatemia et al. (1995): the authors recorded 99 female offspring per lifetime of honey-fed female *T. minutum* compared to 65 female offspring per lifetime of unfed females. In addition, our data showed that the progeny produced early in life is female-biased while the progeny later in life is preponderantly male-biased, as observed for *Trichogramma* spp. (Lim, 1986; Leatemia et al., 1995). The results showing a positive impact of sugar feeding on sex allocation by female parasitoids may have an important ramification for their use in biological control programs.

Our results suggest that sugar feeding may increase lifespan of *P. cerealellae*, in particular in the absence of hosts, and may enhance production of female-biased progeny. The data showing similar longevity for water-provided (sugar-starved) and completely starved *P. cerealellae* in the presence of hosts suggests that host fluid may serve as an alternative to provision of a free water source. Host provision may also have an effect on fecundity of female parasitoids as reported by several authors (Jervis and Kidd, 1986; Van Lenteren et al., 1987). However, it is difficult to test the effect of host feeding on fecundity of *P. cerealellae* since the females are concurrent host feeders utilizing the same individual host for feeding and oviposition (personal observation). The experimental difficulty in separating the opportunity of a parasitoid to host-feed from that to oviposit was alluded to by Heimpel and Collier (1996).

In summary, this study suggests among others, several interesting and sufficiently novel results, including the impact of diet quality on sex allocation and the observation of exploitative host feeding by males paired with females provisioned with hosts. These results offer new insights into parasitoid nutritional ecology and should prove invaluable for the development of efficient mass rearing system for *P. cerealellae*, a prerequisite to its utilization for biological control of stored-product insects.

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References

- Brower, J.H., 1991. Potential host range and performance of a reportedly monophagous parasitoid, *Pteromalus cerealellae* (Hymenoptera: Pteromalidae). *Entomol. News* 102, 231–235.
- Brower, J.H., Smith, L., Vail, P.V., Flinn, P.W., 1996. Biological control. In: Subramanyam, B., Hagstrum, D.W. (Eds.), *Integrated Management of Insects in Stored Products*. Dekker, New York, pp. 223–286.
- Carpenter, J.E., 1995. *Ichneumon promissorius* (Erichson) (Hymenoptera: Ichneumonidae): factors affecting fecundity, oviposition, and longevity. *J. Entomol. Sci.* 30, 279–286.
- Chen, L., Onagbola, E.O., Fadamiro, H.Y., 2005. Effects of temperature, sugar availability, gender, mating, and size on the longevity of phorid fly *Pseudacteon tricuspis* (Diptera: Phoridae). *Environ. Entomol.* 34, 246–255.
- Chow, A., Heinz, K.M., 2005. Using hosts of mixed sizes to reduce male-biased sex ration in the parasitoid wasp, *Diglyphus isaea*. *Entomol. Exp. Appl.* 117, 193–199.
- Ellers, J., 1996. Fat and eggs: an alternative method to measure trade-off between survival and reproduction in insect parasitoids. *Neth. J. Zool.* 46, 227–235.
- Fadamiro, H.Y., Chen, L., 2005. Utilization of aphid honeydew and floral nectar by *Pseudacteon tricuspis* (Diptera: Phoridae), a parasitoid of imported fire ants, *Solenopsis* spp. (Hymenoptera: Formicidae). *Biol. Control* 34, 73–82.
- Fadamiro, H.Y., Heimpel, G.E., 2001. Effects of partial sugar deprivation on lifespan and carbohydrate mobilization in the parasitoid *Macrocentrus grandii* (Hymenoptera: Braconidae). *Ann. Entomol. Soc. Am.* 94, 909–916.
- Fadamiro, H.Y., Chen, L., Onagbola, E.O., Graham, L., 2005. Lifespan and patterns of accumulation and mobilization of nutrients in sugar fed phorid fly *Pseudacteon tricuspis*. *Physiol. Entomol.* 30, 212–224.
- Heimpel, G.E., Collier, T.R., 1996. The evolution of host-feeding behavior in insect parasitoids. *Biol. Rev.* 71, 373–400.
- Heimpel, G.E., Jervis, M.A., 2005. Does floral nectar improve biological control by parasitoids? In: Wäckers, F., van Rijn, P., Bruin, J. (Eds.), *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge University Press, Cambridge, pp. 267–304.
- Heimpel, G.E., Rosenheim, J.A., Kattari, D., 1997. Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus*. *Entomol. Exp. Appl.* 83, 305–315.
- Jacob, H.S., Evans, E.W., 2000. Influence of carbohydrate foods and mating on longevity of the parasitoid *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae). *Environ. Entomol.* 29, 1088–1095.
- Jervis, M.A., Kidd, N.A.C., 1986. Host-feeding strategies in hymenopteran parasitoids. *Biol. Rev.* 61, 395–434.
- Jervis, M.A., Kidd, N.A.C., Fitton, M.G., Huddleston, T., Dawah, H.A., 1993. Flower-visiting by Hymenopteran parasitoids. *J. Nat. Hist.* 27, 67–105.
- Jervis, M.A., Kidd, N.A.C., Heimpel, G.E., 1996. Parasitoid adult feeding and biological control—a review. *Biocontr. News Info.* 17, 11N–26N.
- Leatemia, J.A., Laing, J.E., Corrigan, J.E., 1995. Effects of adult nutrition on longevity, fecundity, and offspring sex ratio of *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae). *Can. Entomol.* 127, 245–254.
- Lee, J.C., Heimpel, G.E., Leibe, G.L., 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomol. Exp. Appl.* 111, 189–199.
- Li, S.Y., Sirois, G., Lee, D.L., Maurice, C., Henderson, D.E., 1993. Effects of female mating status and age on fecundity, longevity and sex ratio in *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *J. Entomol. Soc. B.C.* 90, 61–66.
- Lim, G.T., 1986. Biological studies on *Trichogrammatoidea bactrae fumata* Nagaraja in the laboratory. *J. Appl. Entomol.* 101, 48–54.
- Mbata, G.N., Thomas, A., Fadamiro, H.Y., 2005. Parasitism by *Pteromalus cerealellae* (Hymenoptera: Pteromalidae) on the cowpea weevil, *Callosobruchus maculatus* (Coleoptera: Bruchidae): host density, temperature effects, and host finding ability. *Biol. Control* 33, 286–292.
- Narayanan, E.S., Mookherjee, P.B., 1955. Effect of nutrition on the longevity and rate of reproduction in *Trichogramma minutum* Riley (Chalcidoidea: Hymenoptera). *India J. Entomol.* 17, 376–382.
- Nettles, W.C., 1987. *Eucelatoria bryani* (Diptera: Tachinidae): effects on fecundity of feeding on host. *Environ. Entomol.* 16, 437–440.

- Olson, D.M., Fadamiro, H.Y., Lundgren, J.G., Heimpel, G., 2000. Effects of sugar feeding on carbohydrate and lipid metabolism in a parasitoid wasp. *Physiol. Entomol.* 25, 17–26.
- Parker, R.E., 1979. *Introductory Statistics for Biology*, Second ed. Cambridge University Press, Cambridge.
- Partridge, L., Farquhar, M., 1981. Sexual activity reduces lifespan of male fruitflies. *Nature* 294, 580–582.
- Reznick, D., 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44, 257–267.
- Sagarra, L.A., Vincent, C., Stewart, R.K., 2002. Impact of mating on *Anagyrus kamali* Moursi (Hym., Encyrtidae) lifetime fecundity, reproductive longevity, progeny emergence, and sex ratio. *J. Appl. Entomol.* 126, 400–404.
- SAS Institute, 1998. *JMP Statistics and Graphics Guide*, Version 5.1. SAS Institute, Cary, NC.
- Schmale, I., Wäckers, F.L., Cardona, C., Dorn, S., 2001. Control potential of three Hymenopteran parasitoid species against the bean weevil in stored beans: the effect of adult parasitoid nutrition on longevity and progeny production. *Biol. Control* 21, 134–139.
- Van Lenteren, J.C., van Vianen, A., Gast, H.F., Kortenhoff, A., 1987. The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): food effects on oogenesis, oviposition, lifespan and fecundity of *Encarsia formosa* and other hymenopterous parasites. *Zeitschrift Für Angewandte Entomologie* 103, 69–84.
- Wäckers, F.L., 2001. A comparison of nectar and honeydew sugars with respect to their utilization by the Hymenopteran parasitoid *Cotesia glomerata*. *J. Insect Physiol.* 47, 1077–1084.
- Wheeler, D., 1996. The role of nourishment in oogenesis. *Annu. Rev. Entomol.* 41, 407–431.

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