Effect of Host Age on Progeny Production of *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae) Reared on *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae)

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ABSTRACT

Five host ages of Maize weevil, *Sitophilus zeamais* (Motschulsky) reared on brown rice were examined for progeny production of *Theocolax elegans* (Westwood). Brown rice kernels infested with *S. zeamais* were exposed to a mated female of *T. elegans* after 13, 15, 17, 19 and 21 d following *S. zeamais* introduction. Host stages were determined by measuring head-capsule widths from all the host ages. There was a significant difference ($P < 0.05$) in *T. elegans* progeny production among the different host ages. Total progeny, total female progeny and total male progeny produced by 19-day-old *S. zeamais* larvae were significantly higher ($P < 0.05$) compared to the other host ages. Progeny of *T. elegans* raised on 19-day-old *S. zeamais* larvae had a higher female to male ratio compared to the other host ages. *Sitophilus zeamais* larvae after 13, 15–17 and 19–21 d were found to be second, third and fourth instars, respectively. It was concluded that *T. elegans* can develop on the second, third and fourth instar larvae of *S. zeamais*. However, 19-day-old (fourth instar) *S. zeamais* larvae produced more *T. elegans* progeny with a higher female to male ratio.

Keywords: *Sitophilus zeamais*, *Theocolax elegans*, host ages, progeny production, parasitoid

INTRODUCTION

Rice and maize are important food crops of many countries of the world and are grown for grain which is stored because it cannot be distributed or consumed immediately (Flinn and Hagstrum, 2002; Asl *et al.*, 2009). Storage insect pests feed on harvested grain resulting in economic losses due to spoilage and grain loss and this results in high expenses for chemical treatment and sanitation (Jackai and Adalla, 1997; Tefera *et al.*, 2010). Effective pest management and environmentally friendly approaches must be applied to prevent grain loss and spoilage (Campbell, 2002; Tefera *et al.*, 2010). Chemicals

have adverse effects on consumers and long-term residual effect on the environment (Phillips, 1997; Charlet *et al.*, 2002; Flinn and Hagstrum, 2002; Bale *et al.*, 2007), while biological control agents have no adverse effects on consumers or the environment (Flinn, 1998; Tefera *et al.*, 2010).

Maize weevil, *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) is an important insect pest of stored maize and rice in tropical and subtropical regions (Campbell *et al.,* 1989; Tefera *et al.*, 2010). High infestations of *S. zeamais* were observed in rice stored without controlling the moisture content and with no chemical protectants (Tefera *et al.*, 2010). The first infestation is initiated in the field and the

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weevil develops while grain is in storage (Flinn and Hagstrum, 2002). Infestation occurs when the moisture content is moderate to high and conducive for *S. zeamais* to feed and lay eggs on cereals (Campbell *et al*., 1989; Campbell, 2002). Parasitoids are used successfully throughout the world as biological control agents of many storage insect pests (Ryan *et al*., 1993; Schöller *et al*., 1997).

Parasitoids are biological control agents that feed on or in the tissue of other insects (hosts) and kill their hosts (Charlet *et al*., 2002). Only immature stages of parasitoids are parasitic while adults are free-living, feeding on nectar and honeydew (Flint and Dreistadt, 1998; Bellows and Fisher, 1999). Parasitoids can parasitize eggs, larvae, nymphs, pupae and cocoons (Charlet *et al*., 2002; Wang *et al*., 2003). In 19 species of storage insect pests attacked by 13 species of parasitoids, 163 of 212 estimates of insect pest mortality ranged from 70% to 100%, while in 87 of the estimates, insect pest mortality ranged from 90% to 100% (Hagstrum and Subramanyam, 2006). Thus, the use of natural enemies in controlling storage insect pests can be effective and successful (Flint and Dreistadt, 1998; Burks *et al*., 1999).

Theocolax elegans has been used successfully to control some storage insect pests (Herdman, 1921). Sharifi (1972) reported that *T. elegans* females parasitized pupae and fourth-instar larvae of *S. zeamais* but that study did not compare the impact of different host ages of *S. zeamais* on the progeny production of *T. elegans*. The current study characterized the effect of different host ages of *S. zeamais* to produce progeny of *T. elegans*.

MATERIALS AND METHODS

Insects and grain

Maize weevils were obtained from a 3-month-old stock culture maintained at the National Biological Control Research Centre (NBCRC), Kasetsart University, Thailand. The experiment was established as a randomized complete block design and treatments were replicated 25 times. Weevils were mass-reared on brown rice (*Oryza sativa* L.) at $27 \pm 1°C$ with a relative humidity of $65 \pm 5\%$ and a photoperiod of 12:12 h (light:darkness). Maize weevils were cultured every 2 wk by allowing 50 unsexed adults of the weevils to lay eggs on 100 g brown rice. The brown rice used in the experiment had been frozen at $-20 \pm 2°C$ for at least 3 wk to eliminate contaminates (Tefera *et al*., 2010). The adult weevils were removed from the brown rice after 24 hr. The optimum grain moisture content for storage insects is 13–14% (Haines, 1991). The optimum moisture content was attained by measuring the moisture content using a moisture meter and drying the grain when the moisture content was too high (Tefera *et al*., 2010). *Theocolax elegans* was sourced from a 3-month-old culture of the parasitoid mass-reared at the NBCRC laboratory, Kasetsart University, Thailand. *Theocolax elegans* was mass-reared weekly on fourth-instar larvae of *S. zeamais* at 30°C in the same laboratory. A 24-hour-old female of *T. elegans* was exposed to honey and a male for 24 hr. The *T. elegans* couple was released into 100 g of brown rice infested with fourth-instar larvae of *S. zeamais*.

Effect of host age on progeny production of *Theocolax elegans*

One hundred and twenty-five glass jars, 5.5×15 cm, (one per treatment) each containing 100 g of brown rice with an initial moisture content of 14% were infested with 50 unsexed adults of *S. zeamais* per treatment. The unsexed adults of *S. zeamais* were aged less than 1 mth. *Sitophilus zeamais* oviposit eggs that give a 1:1 progeny sex ratio so the uncontrolled sex ratio did not affect progeny production in each treatment (Campbell *et al.*, 1989). After 24 hr, all adult weevils from the different treatments were removed using a camel-hair brush. *Sitophilus zeamais* eggs were not destroyed when removing the adult weevils

because eggs are oviposited in a slender hole which is covered by a gelatinous secretion that protects and conceals the site of oviposition (Campbell *et al*., 1989). Samples of 100 infested brown rice kernels were selected from each treatment and placed in glass jars, 4×6.5 cm and covered with a filter paper for ventilation.

　　　　Theocolax elegans females and males used in the experiment were aged 48 hr. The wasps were aged by isolating parasitized hosts into vials and inspecting daily for emerged *T. elagans*. After emergence, the 24-hour-old *T. elagans* females were exposed to honey and males for 24 hr before the experiment. The 100 infested brown rice kernels per treatment per jar were exposed to a mated female of *T. elegans* after 13, 15, 17, 19 and 21 d following *S. zeamais* introduction. The 100 infested brown rice kernels provided 100 hosts per treatment per jar. The *Theocolax elagans* females used were removed from each treatment after 24 hr. Only one mated female of *T. elegans* was used per treatment per jar to minimize continuous mating of females with males and to reduce the impact of other females on the sex ratio of *T. elegans* progeny.

　　　　The life cycle of *T. elegans* is about 22 d at 27°C (Sharifi, 1972; Ahmed and Khatun, 1993). Twenty days following the release of *T. elegans*, the numbers of males and females of *T. elegans* produced from each treatment were recorded daily. The total number of males and females of *T. elegans* was used to calculate the total number of *T. elegans* progeny produced from each host age and the sex ratio for each host age. This provided information on the effect of different host ages of *S. zeamais* (13, 15, 17, 19 and 21 d) to support progeny production of *T. elegans*.

Determination of host stages

　　　　To determine host stages, 100 *S. zeamais* adults were allowed to oviposit eggs on 200 g of brown rice. A camel-hair brush was used to remove the 100 *S. zeamais* after 12 hr. After 13, 15, 17, 19

and 21 d following oviposition, five infested brown rice kernels were randomly selected and dissected to obtain *S. zeamais* larvae. Head capsules of the larvae were measured using a calibrated compound microscope (Olympus BH-2 BHS Research Microscope; Olympus Corp.; Shinjuku, Tokyo, Japan) and by taking pictures of a dorsal aspect of the larvae head capsules. The greatest capsule widths from the pictures were used. The head-capsule width of *S. zeamais* at each host age was the average of five head-capsule widths obtained after measuring five *S. zeamais* larvae at 13, 15, 17, 19 and 21 d following oviposition.

Sanitation

　　　　Good sanitation measures are important to prevent contamination of insect colonies by other insect species. A mature colony of *T. elegans* and *S. zeamais* was used to start a new colony (Tefera *et al*., 2010). The old colony was removed from the rearing area because it was a source of contamination. The old colony was cold-treated (frozen at -20 ± 2°C) for 1 hr to ensure that all insects were killed. A plastic bag was used to contain the old colony and prevent live insects from escaping. The work area was kept free of spilled grain because grain can be a source of unwanted insect populations that can infest the stock colony (Tefera *et al*., 2010). The equipment used to maintain the insect colony was washed using a detergent and the equipment was stored in a clean uncontaminated area. The work surfaces were cleaned and disinfested before working on insects (Tefera *et al*., 2010).

Data analysis

　　　　Data on the effect of host age on total progeny production, total female progeny production, male progeny production and head-capsule widths were analyzed using one-way analysis of variance. Means were separated using a least significant difference test at the 95% confidence level. The SPSS statistical package

(Version 20; SPSS Inc.; Chicago, IL, USA) was used to analyze the data.

RESULTS

Effect of host age on total progeny production

Total *T. elegans* progeny production was significantly different among different host ages of *S. zeamais*. Total progeny produced ranged from 256 to 1,335 offspring (Figure 1). The total number of progeny produced by 19-day-old *S. zeamais* larvae was significantly higher compared to the other host ages (Figure 2). This suggests that 19 d following oviposition is the optimum host age compared to the other host ages to produce a high number of *T. elegans* progeny. The number of progeny produced by 17-day-old *S. zeamais*

larvae was the second highest and significantly different from 13-day-old, 15-day-old, 19-day-old and 21-day-old *S. zeamais* larvae (Figure 2). There was no significant difference between total progeny production by 15-day-old and 21-day-old *S. zeamais* larvae. The number of progeny produced by 13-day-old *S. zeamais* larvae was the least and was significantly different from 15-day-old, 17-day-old, 19-day-old and 21-day-old *S. zeamais* larvae (Figure 2).

Effect of host age on total female and male progeny production

The total number of male progeny produced from different host ages was lower compared to total female progeny produced from the different host ages (Figure 3). Total female
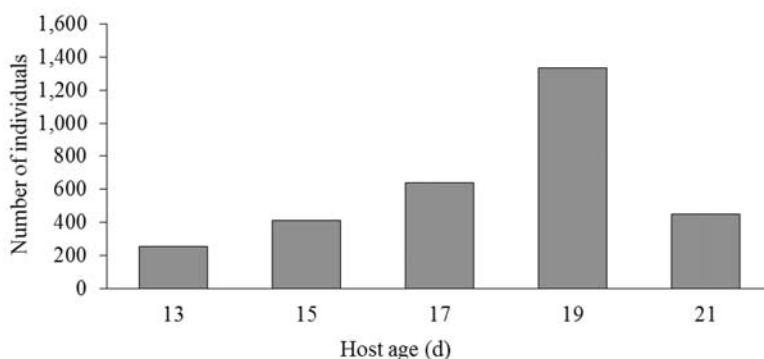

Figure 1 Total *Theocolax elegans* progeny production for different host ages.
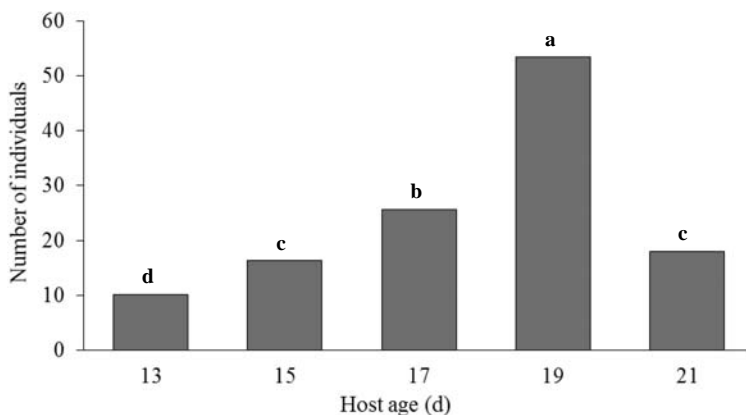

Figure 2 Average *Theocolax elegans* progeny production for different host ages. Bars with the same lowercase letter are not significantly different at $P < 0.05$.

progeny produced ranged from 187 in *T. elegans* reared on 13-day-old *S. zeamais* larvae to 1,084 in *T. elegans* reared on 19-day-old *S. zeamais* larvae (Figure 3). Total male progeny produced ranged from 69 in *T. elegans* reared on 13-day-old *S. zeamais* larvae to 251 in *T. elegans* reared on 19-day-old *S. zeamais* larvae (Figure 3).

The average female *T. elegans* progeny production was significantly different among the different host ages of *S. zeamais*. The average number of female progeny produced by 19-day-old *S. zeamais* larvae was significantly higher compared to the other host ages (Figure 4). The average number of female progeny produced by 17-day-old *S. zeamais* larvae was significantly

different from the other host ages. The average number of female progeny produced by 15-day-old *S. zeamais* larvae was not significantly different from 21-day-old *S. zeamais* larvae but significantly different from the average number of female progeny produced by 17-day-old and 19-day-old *S. zeamais* larvae (Figure 4). There was no significant difference among total female progeny produced by 13-day-old and 15-day-old *S. zeamais* larvae (Figure 4) which suggested that 19 d following oviposition is the optimum host age compared to the other host ages in producing female *T. elegans* progeny.

The average male *T. elegans* progeny production was significantly different among the
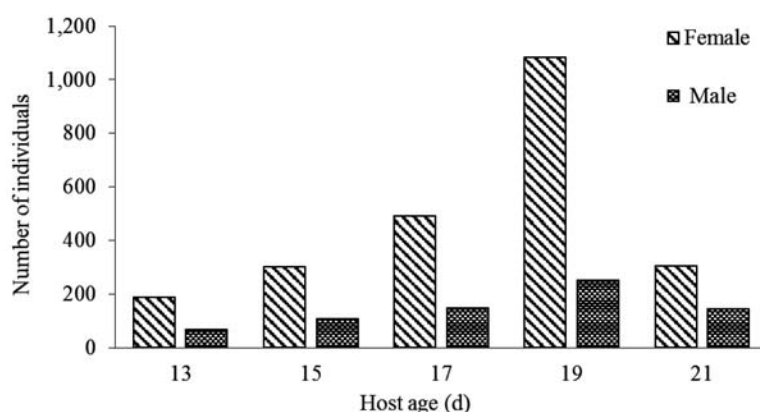

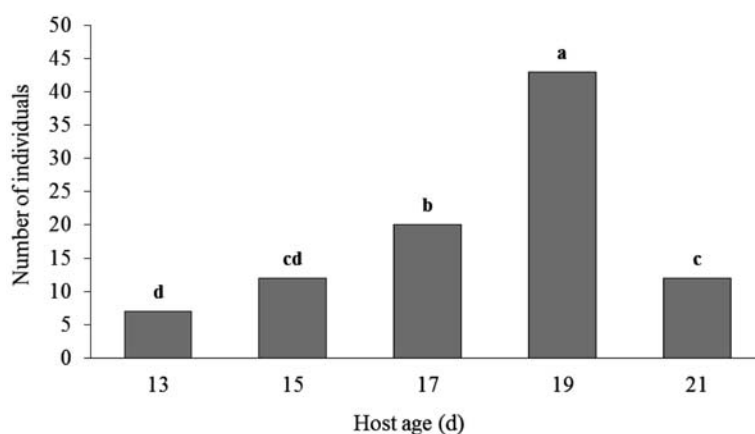**Figure 3** Total male and female *Theocolax elegans* progeny production for different host ages.

Figure 4 Average female *Theocolax elegans* progeny production for different host ages. Bars with the same lowercase letter are not significantly different at $P < 0.05$.

different host ages of *S. zeamais* (Figure 5). The average male progeny production by 19-day-old *S. zeamais* larvae was significantly different from progeny produced by all the other host ages (Figure 5). The average male *T. elegans* produced by 15-day-old, 17-day-old and 21-day-old *S. zeamais* larvae were not significantly different from each other but significantly different from average male *T. elegans* progeny produced by 13-day-old and 19-day-old *S. zeamais* larvae (Figure 5). The average number of male progeny produced by 13-day-old *S. zeamais* larvae was not significantly different from the average number of male progeny produced by 15-day-old *S. zeamais* larvae but significantly different from male progeny produced by 17-day-old, 19-day-old and 21-day-old old *S. zeamais* larvae (Figure 5) which suggested that 19 d following oviposition is the optimum host age compared to the other host ages in producing male *T. elegans* progeny.

Sex ratio

The progeny of *T. elegans* when raised on 19-day-old *S. zeamais* larvae had a higher female to male ratio. The female to male ratios obtained were 2.7, 2.8, 3.3, 4.3 and 2.1 for 13-day-old, 15-day-old, 17-day-old, 19-day-old and 21-day-old *S. zeamais* larvae, respectively (Table 1). A high female to male ratio is important in host finding, parasitism of hosts and in increasing the population of *T. elegans* as only female parasitoids are involved in host finding and parasitism of hosts, while male parasitoids are important in mating but are not involved in host finding and parasitism of hosts (Flinn and Hagstrum, 2001). The 19-day-old *S. zeamais* larvae resulted in an average of 53.4 *T. elegans* progeny, which was higher than the other host ages (Table 1) and had a high female to male ratio.
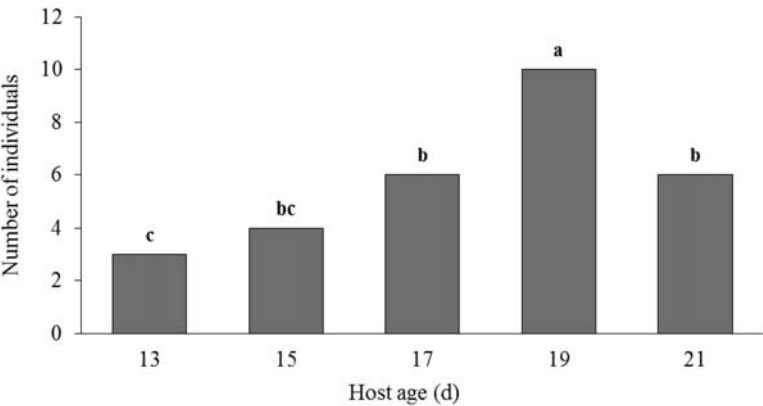

Figure 5 Average male *Theocolax elegans* progeny production for different host ages. Bars with the same lowercase letter are not significantly different at $P < 0.05$.

Table 1 Sex ratio of Theocolax elegans progeny produced from different host ages (n = 25).

S. zeamais age (d)	Mean number of females	Mean number of males	Total	Sex ratio (female to male)
13	7.5	2.8	10.3	2.7
15	12.1	4.4	16.5	2.8
17	19.7	6.0	25.7	3.3
19	43.4	10.0	53.4	4.3
21	12.2	5.8	18.0	2.1

Host stage

The average head-capsule widths of *S. zeamais* larvae were significantly different among the different host ages of *S. zeamais* (Figure 6) being 0.26, 0.41, 0.43, 0.50 and 0.54 mm after 13, 15, 17, 19 and 21 d, respectively (Table 2). The average head-capsule widths of 19-day-old and 21-day-old *S. zeamais* larvae were not significantly different from each other but were significantly different from the other host ages (Figure 6). The average head-capsule widths of 15-day-old and 17-day-old *S. zeamais* larvae were not significantly different from each other but were significantly different from the other host ages (Figure 6). The average head-capsule width of 13-day-old *S. zeamais* larvae was significantly different from the other host ages (Figure 6). The 13-day-old, 15–17-day-old and 19–21-day-old *S. zeamais* larvae were second, third and fourth instars, respectively (Table 2). However, there were no results on the head-capsule widths of first instar larvae of *S. zeamais* because data were collected at 13, 15, 17, 19 and 21 d after oviposition.

DISCUSSION

Head-capsule width as an indicator of larval instar numbers in *S. zeamais* is more efficient compared to using larval weights (O'Donnell, 1967). O'Donnell (1967) reported that head-capsule widths of *S. zeamais* varied in the ranges 0.16–0.22, 0.25–0.29, 0.34–0.43 and 0.49–0.54 mm for first, second, third and fourth instars, respectively. The current study showed that the second, third and fourth instars head-capsule widths of *S. zeamais* larvae were consistent with the ranges reported by O'Donnell (1967). The first, second, third and fourth instars and the pre-pupal stages of *S. zeamais* took 3, 5, 6, 3, and 3 d, respectively (O'Donnell, 1967). *Sitophilus*

Table 2 Stage and mean head-capsule width of *Sitophilus zeamais* at different host ages.

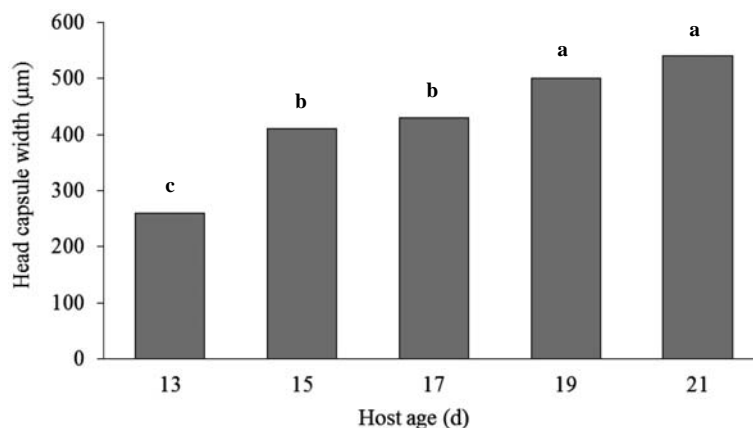| Host age (d)	Head-capsule width (mm)	Host stage
13	0.26	Second instar
15	0.41	Third instar
17	0.43	Third instar
19	0.50	Fourth instar
21	0.54	Fourth instar

Figure 6 Average head-capsule widths of *Sitophilus zeamais* larvae for different host ages. Bars with the same lowercase letter are not significantly different at $P < 0.05$.

zeamais larvae after 13, 15–17 and 19–21 d were found to be second, third and fourth instar larvae, respectively.

Factors affecting progeny production in parasitoids include: host density, host age, availability of food, parasitoid age, insemination and the oviposition period (Riddick, 2003). However, the current study focused on the effect of host age on progeny production by *T. elegans* as all the other factors affecting progeny production were not varied. Thus the current work did not study the effect of host density, availability of food, parasitoid age, insemination and oviposition period on progeny production by *T. elegans*.

Theocolax elegans females can parasitize fourth instar and pupae of *S. zeamais* (Sharifi, 1972) and the current study showed that *T. elegans* can develop on second, third and fourth instar larvae of *S. zeamais* with a significantly high progeny production when *T. elegans* was reared on 19-day-old *S. zeamais* larvae. The results from the host stages study confirmed that 19-day-old *S. zeamais* larvae were in the fourth instar which results concurred with Sharifi (1972) who reported that *T. elegans* females parasitized fourth instar larvae of *S. zeamais*. Second and third instar larvae of *S. zeamais* could produce progeny but more progeny were obtained when fourth instar (19-day-old) larvae of *S. zeamais* were parasitized.

The high progeny production by 19-day-old (fourth instar) *S. zeamais* results from the fact that grain kernels infested with 19-day-old *S. zeamais* larvae produce a special texture. The special texture stimulates oviposition in the wasp; hence more progeny were produced by 19-day-old *S. zeamais* larvae. This implies that *T. elegans* females can differentiate on the appropriate host size (within the same host stage) that stimulates oviposition in the wasp where more parasite progeny can be produced. The other host ages (13, 15, 17 and 21 d) can produce progeny because *T. elegans* can locate hosts in grain kernels but the texture perceived during drumming did not

stimulate oviposition. When the host age did not stimulate oviposition, the host was usually stung to reduce host immune defense (Press, 1992).

Sitophilus zeamais larvae at 21 d following oviposition were found to be in the fourth instar larval stage. At 21 d following oviposition, *S. zeamais* larvae are expected to produce more progeny as the larvae are still in the fourth instar. However, *T. elegans* reared on 21-day-old *S. zeamais* larvae produced total progeny not significantly different from *T. elegans* reared on 15-day-old *S. zeamais* larvae. The current study found that 15-day-old *S. zeamais* larvae were in the third instar larval stage—a result that did not concur with Sharifi (1972) but suggests that the resource quality (host larvae) at 21 d following oviposition was declining and thus affected the number of parasites emerging later. The number of progeny produced by 21-day-old *S. zeamais* larvae was significantly lower than progeny produced by 19-day-old *S. zeamais* larvae. This implies that *T. elegans* parasitized more fourth instar larvae of *S. zeamais* at 19 d following oviposition compared to the other host ages and it can be concluded that the timing of the release of *T. elegans* to coincide with the same host stage and age is very important.

A female *T. elegans* can parasitize up to six hosts per day (Flinn and Hagstrum, 2001) but the results from the current experiment were not consistent with Flinn and Hagstrum (2001) because female *T. elegans* produced an average of 10.24, 16.44, 25.56, 53.4 and 18 *T. elegans* progeny at 13, 15, 17, 19 and 21 d, respectively. The results were observed after one female was exposed to 100 infested brown rice kernels for 24 hr.

Theocolax elegans females were exposed to males for 24 hr before the experiment to allow inseminaiton. *Theocolax elegans* reproduction is arrhenotokous—the male offspring are haploid and the female offspring are diploid (Williams and Floyd, 1971). This means that uninseminated females of *T. elegans* can produce male progeny

parthenogenically; males were produced even though the females were inseminated. Insemination of female wasps does not ensure that all eggs are fertilized in a parthenogenetic species as the inseminated females store sperm in spermathecal capsules and can choose the sex of their progeny by releasing or not releasing sperm when an egg passes through the oviduct with an unfertilized egg developing into a male whereas a female develops when sperm are released to fertilize an egg passing through the oviduct (Williams and Floyd, 1971). Thus, females can control their progeny sex ratio by controlling egg fertilization and parasitic Hymenoptera typically have skewed sex ratios (King, 1993) which explains why a high number of females compared to males was observed in the current study.

Sitophilus zeamais is an agricultural pest and a host of T. elegans (King, 1993). Release of parasitoids to control agricultural pests is important in a biological control program and so a high number of T. elegans females compared to T. elegans males is important in the control of S. zeamais. The sex ratio of T. elegans progeny is affected by environmental factors which are important when mass-rearing the parasitoid (King, 1993). Theocolax elegans females select their progeny sex ratio to pass their genes to future generations. Two environmental conditions affecting progeny sex ratio are resources that will be available to the progeny and the number of female parasitoids present (King, 1993).

Theocolax elegans is a pteromalid wasp known to manipulate its progeny sex ratio as a result of environmental conditions (King, 1993). Most pteromalid wasps produce a high proportion of males in smaller hosts (King, 1993). The current results depict an increase in the progeny sex ratio as the size or quality of the host increased (from 13-day-old to 19-day-old S. zeamais larvae). The results concurred with King (1993) because a high number of males (compared to the total progeny produced) were produced by smaller hosts. A decrease in the number of male progeny (compared to the total progeny produced) was obtained as the size of the host increased resulting in a higher proportion of females than males in bigger hosts.

However, when 21-day-old S. zeamais larvae were used to mass-rear T. elegans, the progeny sex ratio decreased. A reduction in the progeny sex ratio at 21 d following oviposition suggests that the number of males (compared to the total progeny produced) increased hence reducing the progeny sex ratio. While these results did not concur with King (1993), they suggest that the resource quality (host larvae) at 21 d following oviposition was declining and thus affected the sex of the parasitoids emerging later. The results showed that 19-day-old S. zeamais larvae had a high female to male ratio. The high proportion of females compared to males when 19-day-old S. zeamais larvae were used to mass-rear T. elegans suggests that at 19 d following oviposition, the host quality or size is conducive for producing a higher number of females compared to males.

Female parasitoid wasps produce a higher proportion of male progeny when other females are present than when alone (King, 1993). The current experiment used only one inseminated T. elegans female per unit so it was not possible to determine the effect of other females on the sex ratio of the T. elegans progeny produced.

CONCLUSION

Host age played an important role in the progeny production of T. elegans when reared on S. zeamais larvae. This was shown by the significantly high progeny production when T. elegans was reared on 19-day-old S. zeamais larvae. T. elegans can develop on second, third and fourth instar larvae of S. zeamais as T. elegans progeny were produced by these host stages. However, the highest progeny production was observed when 19-day-old (fourth instar) S.

zeamais larvae were used to mass-rear *T. elegans*. Thus it can be concluded that the timing of the release of *T. elegans* within the same host stage is very important. This explains the importance of host age when timing the release of *T. elegans*.

ACKNOWLEDGEMENTS

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