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SHORT COMMUNICATION

Parasitism of the Coffee Berry Borer *Hypothenemus hampei* by *Trichogramma pretiosum* in the Laboratory

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Parasitism of the coffee berry borer, Hypothenemus hampei *(Ferrari) by* Trichogramma pretiosum *Riley resulted in high mortality of developing parasitoids and a low prevalence of adult emergence. A laboratory colony of* T. pretiosum *reproducing in* H. hampei *failed after three generations. Adult female* T. pretiosum *that developed in* H. hampei *were smaller and produced fewer eggs than conspecifics that developed in a standard lepidopteran host,* Sitotroga cerealella *(Olivier). Parasitoids that emerged from* H. hampei *preferentially parasitized* S. cerealella *over* H. hampei*. We conclude that* T. pretiosum *has little potential for biocontrol of the coffee berry borer.*

Keywords: Hypothenemus hampei*,* Sitotroga cerealella*, novel host, parasitoid fecundity, development, body size, longevity.*

The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) is the principal pest of coffee worldwide (Le Pelley, 1968). The eggs and immature stages of the insect develop in galleries inside the coffee berry. The cryptic development of the pest means that even with large scale releases of bethylid or eulophid parasitoids, an adequate level of pest control can be difficult to attain (Barrera *et al.*, 1990; Pérez-Lachaud, 1998).

Many species of *Trichogramma* (Hymenoptera: Trichogrammatidae) are amenable to laboratory rearing and are frequently used for the inundative biological control of lepidopterous pests (Li, 1994). Species of *Trichogramma* have been observed parasitizing the eggs of most major insect orders (Smith, 1996), although parasitism of the coffee berry borer by *Trichogramma* spp. has not been reported.

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The present study aimed to determine whether or not there exist barriers to parasitism or progeny development of *Trichogramma pretiosum* Riley in eggs of the coffee berry borer. We also examined the consequences of development in this host on a selection of parasitoid fitness correlates including fecundity, longevity, and body size. Parasitoid reproduction in *H. hampei* was compared to a standard laboratory host, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), over a period of two generations. We selected *T. pretiosum* for this study because of its polyphagous habits (Consoli & Parra, 1996) and because it is readily available to farmers in Mexico through commercial suppliers of natural enemies.

Eggs of *H. hampei* were obtained from infested coffee berries (*Coffea arabica* L.), collected within 40 km of Tapachula, Chiapas, Mexico. Eggs of *S. cerealella* were obtained from a laboratory culture maintained in the Centro Internacional de Investigación y Capacitación Agropecuaria (CIICA), Frontera Hidalgo, Chiapas, Mexico. The eggs of *H. hampei* were slightly larger than those of *S. cerealella*: *H. hampei* egg length (mean $\pm$S.E.) 0.648 ± 0.009 mm, egg width 0.323 ± 0.005 mm, compared to *S. cerealella* egg length 0.633 ± 0.035 mm, egg width 0.250 ± 0.015 mm. Adult *T. pretiosum* were obtained from a continuous culture held in CIICA using *S. cerealella* as hosts. All experiments were performed at $26 \pm 2^{\circ}$C, $85 \pm 10\%$ RH and continuous light.

To determine the age of egg preferred by the parasitoid, *H. hampei* eggs of < 24 h, and 1–2, 2–3 and 3–4 days were simultaneously offered to *T. pretiosum*. The host eggs were collected at 24-h intervals such that age classes did not overlap. Twenty eggs of each age class were placed in 16 groups of five distributed as a 4×4 Latin square on a 5-cm diameter damp filter paper disk (80 eggs in total). The filter paper was placed in a 5.5-cm diameter Petri dish, and eight mated *T. pretiosum* females with no prior ovipositional experience were introduced. After 24 h of exposure, the adult wasps were removed and the eggs were incubated for 15 days. Experimental eggs were then examined for signs of parasitoid emergence. Eggs that did not show signs of eclosion were dissected to determine the presence of dead immature stages. This experiment was performed three times.

To compare parasitoid development in each host species, groups of approximately 250 *H. hampei* eggs, 1–3 days old, were placed in a glass cage ($50 \times 50 \times 150$ cm tall) containing approximately 100 000 *T. pretiosum* adults (0.46 proportion male) for a period of 2 h. The eggs were then removed and development of the parasitoid was observed by dissection of between 10 and 50 parasitized eggs at 24-h intervals, up to 8 days post-parasitism. The body length and width at the widest point for each growth stage was measured using a binocular compound microscope fitted with a calibrated eyepiece graticule. An identical experiment was simultaneously performed using *S. cerealella* as hosts.

The effects of host on adult parasitoid reproduction, longevity and size were determined as follows. A single group of between 60 and 382 *H. hampei* eggs (depending on their availability from the field material), 1–3 days old, was placed on a 5-cm diameter damp filter paper disk inside the 1.5-m tall glass cage containing $\sim 100\,000$ *T. pretiosum* adults. After 24 h, the eggs were removed and incubated to allow parasitoid development. This process was repeated once a day for 10 days; data from these 10 replicates were then pooled to give results for one generation. After 7 days of incubation, 1 day prior to the beginning of adult parasitoid emergence, each cohort of parasitized eggs was placed in a 14-cm diameter Petri dish containing 100 eggs of *H. hampei*, 1–3 days old, on damp filter paper. To obtain a second generation, the parasitoids were allowed to emerge, mate and parasitize the eggs offered over a period of 3 days. The *H. hampei* eggs were replaced daily. For each batch of eggs, the percent parasitism, percent adult emergence and the secondary sex ratio was noted. The size of parasitoids that emerged from *H. hampei* eggs was determined by measuring the length of the hind tibia of 25 randomly selected female parasitoids, using an eyepiece graticule to an accuracy of 0.01 mm.

To assess female fecundity and longevity, 10 mated females were selected from each parasitoid generation. These females were individually offered 1–3-day-old *H. hampei* eggs

in a 5.5-cm Petri dish containing a damp filter paper disk and a drop of 50% honey solution. In previous studies, a marked decrease in fecundity was observed with parasitoid age. In order to maximize the limited supply of *H. hampei* eggs, the number of *H. hampei* eggs offered on each day was steadily reduced from 25 eggs on day 1, 20 eggs on day 2, 15 eggs on day 3, 10 eggs on day 4, and five eggs thereafter until death of the parasitoid. Fecundity was calculated as the total number of eggs parasitized by each female during her lifetime. The above procedures were repeated for parasitoids exposed to *S. cerealella* eggs. The experiment ran for two parasitoid generations.

The behaviour of *T. pretiosum* toward eggs of each host species was determined for each parasitoid generation obtained in the previous experiment. Depending on availability, between five and 10 female parasitoids were placed individually in a 5.5-cm diameter Petri dish containing a damp filter paper disk, two 1-cm^2 squares of black paper, 2 cm apart. On one square, four groups of three *H. hampei* eggs were placed in each corner of the square (12 eggs in total). Identical groups of *S. cerealella* eggs were placed on the other square. Each female was observed once every 30 min for a period of 7.5 h and her activity was classified as not in contact with the host, in contact with the host or parasitizing the host. After the observation period, each female was removed and the eggs were incubated for 15 days after which parasitism and adult emergence were recorded.

Egg age preferences and the size of immature and adult parasitoids were analyzed by ANOVA followed by Tukey test for mean separation. In all cases, the error distribution and homogeneity of variance (homoscedasticity) were carefully examined for evidence of deviation from the assumptions of an ANOVA. The numbers of parasitized eggs that failed to emerge were subjected to a χ^2-test for each developmental stage of the parasitoid. Percent parasitism and percent emergence data were arcsine transformed prior to ANOVA and mean separation. Adult sex ratios were compared between species by χ^2-test. The results of the two-host choice experiments were analyzed with the paired t-test.

There was a highly significant effect of *H. hampei* egg age on parasitism by *T. pretiosum* ($F_{(3,24)} = 40.4$, $P < 0.001$). No parasitic activity was observed towards 3–4-day-old *H. hampei* eggs. In contrast, a similar but small number of eggs were parasitized in the three younger age classes (2.4 ± 0.39 <1 day old; 2.9 ± 0.43 1–2 days old; 2.8 ± 0.40 2–3 days old, mean $\pm$S.E.). This represented 12–14% parasitism. Emergence of parasitoid adults from the exposed *H. hampei* eggs was low (1.7–16.7%). However, egg age affected parasitoid emergence ($F_{(3,24)} = 8.67$, $P < 0.001$) with significantly more adults emerging from 1–2-day-old eggs (0.40 ± 0.14 adults per replicate, mean $\pm$S.E.) and 2–3-day-old age eggs (0.80 ± 0.20 adults per replicate) compared to other age classes. Only one parasitoid emerged from a total of 60 eggs of the <1 day age class. Rejection of older hosts by *T. pretiosum* has also been observed in conventional lepidopteran hosts (Reznik & Umarova, 1990; Monje *et al.*, 1999) although this may be modulated by previous experience of hosts of different ages (Reznik *et al*., 1997). The probability of parasitoid survival in older lepidopteran hosts is reduced compared to that of young hosts (Ruberson & Kring, 1993), underscoring the importance of host age discrimination to the reproductive success of the parasitoid.

Dissection of *H. hampei* eggs exposed to parasitoids indicated that the number of *T. pretiosum* that died as immature stages was elevated but did not differ significantly among host age classes (25/28 for <1-day-old eggs, 25/30 for 1–2-day-old eggs, 20/24 for 2–3-day-old eggs) ($\chi^2 = 0.540$, d.f. $= 2$, $P = 0.763$). In contrast, the number of *T. pretiosum* that died in *S. cerealella* eggs was minimal. The average parasitoid development time from egg to adult was 8 days in *H. hampei* and *S. cerealella* eggs alike (Table 1). The size of each stage of the developing parasitoid tended to be slightly larger in *H. hampei* than in conspecifics developing in *S. cerealella* (Table 1), an effect that was most evident at 2 and 3 days post-parasitism. The polyphagous habits and the successful rearing of *T. pretiosum* on artificial media (Consoli & Parra, 1996) indicate that the immature stages of this species are tolerant to a broad range of developmental conditions (Grenier, 1994; Greenberg *et al.*, 1998). It is

TABLE 1. Stage and body size of immature *T. pretiosum* at daily intervals post-parasitism in eggs of *H. hampei* and *S. cerealella*

				Immature parasitoid body size[a] (mm) mean ± S.E.			
Age (days post parasitism)	*N*	Host	Developmental stage	Length		Width	
1	10	*H. hampei*	Egg	0.16 ± 0.006	a	0.08 ± 0.003	b
	10	*S. cerealella*	Egg	0.19 ± 0.006	b	0.09 ± 0.002	a
2	10	*H. hampei*	Larva	0.48 ± 0.009	a	0.32 ± 0.006	a
	10	*S. cerealella*	Larva	0.41 ± 0.009	b	0.25 ± 0.006	b
3	10	*H. hampei*	Prepupa	0.47 ± 0.009	a	0.31 ± 0.006	a
	10	*S. cerealella*	Prepupa	0.42 ± 0.025	a	0.24 ± 0.009	b
4	10	*H. hampei*	Prepupa	0.46 ± 0.016	a	0.30 ± 0.006	a
	10	*S. cerealella*	Prepupa	0.47 ± 0.016	a	0.27 ± 0.006	a
5	10	*H. hampei*	Pupa	0.50 ± 0.009	a	0.27 ± 0.006	a
	10	*S. cerealella*	Pupa	0.45 ± 0.009	b	0.25 ± 0.009	a
6	10	*H. hampei*	Pupa	0.49 ± 0.003	a	0.26 ± 0.003	a
	10	*S. cerealella*	Pupa	0.46 ± 0.016	a	0.24 ± 0.009	a
7	10	*H. hampei*	Pupa	0.50 ± 0.012	a	0.26 ± 0.003	a
	10	*S. cerealella*	Pupa	0.47 ± 0.009	a	0.26 ± 0.006	a
8	50	*H. hampei*	Adult[b]	–		–	
	50	*S. cerealella*	Adult[b]	–		–	

[a]Means in the same column followed by the same letter do not differ significantly for comparisons within days (Tukey test $P < 0.05$).
[b]Size of adult parasitoids given in Table 2.

perhaps then, not surprising that this species was able to develop in *H. hampei* eggs, a host from which it has not been previously reported. However, it was clear from the poor survival of the juvenile stages and the low adult eclosion that *H. hampei* was not a particularly good host for *T. pretiosum*.

In the first generation, percent parasitism of *H. hampei* was high (90.5%), but was significantly less than that observed when *S. cerealella* eggs were offered as hosts ($F_{(1,18)} = 6.89$, $P = 0.017$). A substantially lower percentage of adults emerged from parasitized *H. hampei* eggs than from *S. cerealella* ($F_{(1,18)} = 53.2$, $P < 0.001$) (Table 2). In the second parasitoid generation, the percent parasitism of *H. hampei* eggs fell markedly (to 34.6%), whereas parasitism of *S. cerealella* remained high (84.9%) ($F_{(1,18)} = 43.5$, $P < 0.001$). The percent eclosion of adults from *H. hampei* eggs was extremely low (1.32%) compared to *S. cerealella* (73.0%) ($F_{(1,18)} = 215$, $P < 0.001$) (Table 2). There were insufficient parasitoids from *H. hampei* eggs to carry out percent parasitism and emergence studies for a third generation.

When offered a choice of two or more species, laboratory studies involving *Trichogramma* spp. usually reveal a distinct preference for a particular host species (Schmidt, 1994), as was the case in this study. Size and shape differences between *S. cerealella* and *H. hampei* may have been highly influential in this respect. Host size may be particularly important for idiobiont species, such as *Trichogramma*, for which the host represents a fixed resource (Salt, 1935; Grenier *et al.*, 2001). In general, larger hosts tend to be preferred over smaller

hosts as they can be used to produce larger, or a greater number of, progeny (Godfray, 1994). However, the size of the host used for rearing, in this case *S. cerealella*, can affect host size preferences in the adult parasitoid (Nurindah *et al.*, 1999), and egg shape is recognized to be a key characteristic for host discrimination (Salt, 1935). Greenberg *et al*. (1998) showed that the body size of adult *T. pretiosum* was positively correlated with fecundity and also affected the size of eggs parasitized; larger females parasitized a higher percentage of large eggs. These observations may be a direct consequence of differences in the length of the ovipositor in small and large conspecific parasitoids which can determine the ability to parasitize hosts with thick egg chorions (Grenier *et al.*, 2001). Apart from the size, shape and age of the egg, other factors have been shown to influence host recognition and acceptance including the surface odour (Salt, 1937; Norlund *et al*., 1987), the toughness of the chorion (Rajendram, 1978), and biochemical cues from inside the egg (Nettles *et al*., 1985). All these factors are likely to have been markedly different for the two host species that we compared given that they represent different insect orders.

The secondary sex ratio of parasitoids from *H. hampei* eggs was moderately female biased ($F(1) = 0.38$ male; $F(2) = 0.42$ male). The sex ratio of parasitoids emerging from *S. cerealella* eggs was 0.52–0.43 male in the first and second generations, respectively. The secondary sex ratios of parasitoids emerging from these two hosts was significantly different from each other only in the first generation ($\chi^2 = 3.96$, d.f. $= 1$, $P < 0.050$).

The effect of host on parasitoid fitness correlates was very clear. Longevity of adult females from each host did not differ significantly when compared within each generation, although female parasitoids from *H. hampei* showed a dramatically reduced fecundity compared to those from *S. cerealella* in the first ($F_{(1,18)} = 9.82$, $P < 0.006$) and the second ($F_{(1,13)} = 31.6$, $P < 0.001$) generations (Table 2). Female parasitoids that emerged from *H. hampei* were significantly smaller than those that developed in *S. cerealella* in the first ($F_{(1,48)} = 8.78$, $P < 0.005$) and the second generations ($F_{(1,48)} = 5.70$, $P = 0.021$), as determined by tibia length.

Host species can have marked effects on correlates of parasitoid fitness (Pavlik, 1993). For example, adult body size (particularly wing size, shape and asymmetry) can affect the reproductive success of the parasitoid in the field (Bennett & Hoffmann, 1998). As such, the host used for rearing has a direct bearing on the efficacy of the parasitoid as a biocontrol agent (Corrigan & Laing, 1994; Greenberg *et al.*, 1998).

When offered eggs of *H. hampei* and *S. cerealella* together, the first generation of parasitoids that emerged from *H. hampei* showed a clear preference to parasitize *S. cerealella*. Parasitoid contact with a host was 10 times more frequent on *S. cerealella* eggs (26% of observations) compared to *H. hampei* eggs (2.6% of observations) ($t = 4.61$, d.f. $= 9$, $P = 0.001$); the remaining observations involved no contact with either host. The resulting mean percent parasitism was accordingly higher in *S. cerealella* eggs (80.1 ± 9.6) compared to *H. hampei* (34.5 ± 9.8) ($t = 3.56$, d.f. $= 9$, $P = 0.006$). Percent parasitoid emergence was also significantly higher in *S. cerealella* (72.9 ± 10.9) compared to *H. hampei* (3.1 ± 2.2) ($t = 6.31$, d.f. $= 9$, $P < 0.001$). Second-generation parasitoids emerging from *H. hampei* eggs manifested a similar but low level of activity; the frequency of parasitic behaviour on *H. hampei* and *S. cerealella* eggs was low (4.0 and 16.0%, respectively), and was not significantly different between host species ($t = 1.87$, d.f. $= 4$, $P = 0.137$). The percent parasitism observed in *S. cerealella* (74.7 ± 8.7) was again greater than that of *H. hampei* (28.9 ± 18.8) ($t = 3.53$, d.f. $= 4$, $P = 0.024$). Similarly, percent adult eclosion was significantly higher in *S. cerealella* (59.5 ± 6.2) than in *H. hampei* (15.5 ± 9.2) ($t = 4.23$, d.f. $= 4$, $P = 0.013$).

Through a series of artificial selection procedures it may be possible to obtain a culture of *T. pretiosum* adapted to parasitism of *H. hampei*. For this, it would be necessary to ensure a high degree of genetic heterogeneity in the initial *T. pretiosum* culture, a factor that may have been influential in the present study. Our parasitoid culture had been maintained for

TABLE 2. Changes in percent parasitism, adult eclosion, female longevity, fecundity, tibia length and secondary sex ratio in two sequential generations of *T. pretiosum* reared in *H. hampei* or *S. cerealella* eggs (all figures are means ± S.E.)

Generation	Host	Percent parasitism	Percent adult eclosion	Longevity (days)	Fecundity (eggs/female)	Female tibia length (mm)	Sex ratio (proportion male)
F1	*H. hampei*	90.5 ± 0.95a	36.7 ± 6.82a	1.4 ± 0.16a	3.7 ± 1.34a	0.141 ± 0.002a	0.38a
	S. cerealella	95.5 ± 0.60b	89.1 ± 1.43b	2.1 ± 0.58a	25.1 ± 6.70b	0.149 ± 0.002b	0.52b
F2	*H. hampei*	34.6 ± 5.63a	1.3 ± 0.47a	1.4 ± 0.24a	1.8 ± 0.37a	0.140 ± 0.002a	0.42a
	S. cerealella	84.9 ± 3.83b	73.0 ± 4.52b	2.3 ± 0.33a	31.7 ± 3.68b	0.148 ± 0.002b	0.43a

[a]Means in the same column followed by the same letter did not differ significantly for comparisons within each generation (ANOVA, Tukey test, $P < 0.05$).
[b]Sex ratio data from each host were compared with one another within each generation by χ^2-test.

approximately 40 generations on *S. cerealella* eggs and was probably of low genetic heterogeneity, thus reducing the probability of selecting individuals better adapted to development in *H. hampei* eggs. An additional barrier to the successful use of *T. pretiosum* in the field for control of *H. hampei* relates to the ability of this minute wasp to find infested coffee berries, enter and parasitize *H. hampei* eggs therein. However, due to the poor efficiency of reproduction, and the low viability of adult parasitoids that emerged from *H. hampei* eggs in the laboratory study, we decided that field or glasshouse experiments on parasitoid efficacy in biocontrol of this pest were not merited. We conclude that *T. pretiosum* is unlikely to be an effective control agent for the coffee berry borer.

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