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HOST PREFERENCE OF THE FACULTATIVE HYPERPARASITOID *TETRASTICHUS HOWARDI (HYM.: EULOPHIDAE)*

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Tetrastichus howardi (Olliff) preferred the lepidopteran hosts, *Chilo partellus* (Swinhoe) (Pyralidae) and *Helicoverpa armigera* (Hübner) (Noctuidae) to their parasitoids, *Xanthopimpla stemmator* (Thunberg) (Hymenoptera: Ichneumonidae) and *Palexorista laxa* (Curran) (Diptera: Tachinidae). If *T. howardi* had previously experienced parasitising a certain host, its preference for that host increased, but not significantly. When reared on a certain host, the preference for that host increased. *T. howardi* showed no preference to any particular age of its hosts. *T. howardi* was able to discriminate between parasitised and unparasitised hosts, initially preferring parasitised hosts, but two days later preferring unparasitised hosts.

KEY-WORDS: Host preference, *Tetrastichus howardi,* facultative hyperparasitoid.

The lepidopterous stem borers *Chilo partellus* (Swinhae) (Pyralidae) and *Busseola fusca* (Fuller) (Noctuidae) are the most damaging of all the pests of maize and grain sorghum in South Africa (Skoroszewski & Van Hamburg, 1987).

Tetrastichus howardi (Olliff) was introduced into South Africa from the Philippines, as a potential biocontrol agent of these borers (Kfir *et al.*, 1993). *T. howardi* is a gregarious pupal endoparasitoid with a broad distribution in Asia, Australia and Mauritius (Boucek, 1988). In the Philippines it attacks the Asiatic rice borer, *Chilo suppresalis* (Walker) (Shepard, personal communication, International Rice Research Institute, Box 933, Manila, Philippines).

As *T. howardi* was shown to be polyphagous and hyperparasitic in the laboratory (Cherian & Subramaniam, 1940; Rudriah & Sastry, 1959; Bennett, 1965; Kfir *et al.*, 1993), we decided to examine its host preference and host discrimination in quarantine before releases in the field.

MATERIALS AND METHODS

T. howardi was reared in the laboratory on *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). All experiments were conducted with 2-day old mated parasitoids in a controlled environment room at 24 ± 2°C and 60 ± 10% RH. Parasitoids were cultured in ventilated wooden cages (300 × 430 × 340 mm) with honey and water.

HOST PREFERENCE

Tests were carried out to establish if *T. howardi* showed a preference for either of the lepidopteran pests, *C. partellus* and and *H. armigera,* or their respective parasitoids, *Xanthopimpla stemmator* (Thunberg) (Hym.: Ichneumonidae) and *Palexorista laxa* (Curran) (Dipt.: Tachinidae).

Both long (5 day) and short (200 min) term preference tests were conducted with *T. howardi*. Long term tests were done to observe whether host preference developed or changed over a period of time, and short term tests enabled us to see if any initial preference existed.

In long term tests, *T. howardi* females were kept singly with males in ventilated glass vials (25 mm diameter; 100 mm long) each containing 4 pupae (2 from each host tested). All hosts were removed and replaced with fresh ones every 24 h for 5 days. Emergence from each host was recorded. A total of 30 replications of each pairwise comparison was conducted.

Data were analyzed using Chi-square analyses and the Generalised Linear Model (GLM) for contingency tables (Dobson, 1983). GLM with the log-normal distribution for contingency tables was used, as results are more meaningful and can be determined as odds ratios (U). Odds ratios more clearly signify degrees of preference and are calculated by the formula:

$$u = e^{x},$$

where x is the estimate of the regression coefficient. This is a measure of the relative likelihood of an event occurring for each of two different groups. It is an approximate method based on appropriate conditional likelihood functions (Dobson, 1983).

In short term tests, *T. howardi* females were first held for a day with honey only or with host pupae as well (either of the 2 hosts tested). This was for the purpose of determining the influence of previous experience on host selection. Parasitoids were then placed separately in Petri dishes (65 mm diameter; 12 mm hight). Each dish contained 4 host pupae (2 from each host tested). Females were observed at 10 min intervals for the next 200 min and their position noted if they were on either host. A 10 min interval for observations was deemed sufficient as mean oviposition time of *T. howardi* was 112 min.

The preference of *T. howardi* females, reared from *C. partellus* or *H. armigera,* and from *H. armigera* or *P. laxa* was compared. Data were analyzed in a similar way as for the long term test.

Influence of host age on preference

T. howardi females were placed individually in Petri dishes. Each Petri dish contained 4 hosts (all either *C. partellus* or *H. armigera*): 2 of 1-day old and 2 of 5-day old pupae. Parasitoids were observed at 10 min intervals for the next 200 min and their position noted if they were on any of the hosts.

Host discrimination

Short term preference tests were conducted with *T. howardi* to determine if the females discriminate between parasitised and unparasitised hosts. The method and procedure were similar to those of the short term host preference tests. *H. armigera* pupae were exposed to *T. howardi* in a rearing cage for about 20 h and then used in the experiments, immediately after parasitisation and 1, 2, 5 and 12 days after parasitisation. T. howardi females were previously experienced with parasitised hosts, unparasitised hosts, or were inexperienced.

RESULTS AND DISCUSSION

Host preference

According to Chi-square analyses *T. howardi* developed a significant preference for *C. partellus* over *H. armigera* ($\chi^2 = 15.05$; $P = 0.005$), and over *P. laxa* ($\chi^2 = 10.01$;

P = 0.04). *T. howardi* showed an insignificant preference for *C. partellus* over its parasitoid, *X. stemmator* ($\chi^2 = 7.38$; P = 0.116). *T. howardi* showed an overwhelmingly significant preference for *H. armigera* over *P. laxa*. Chi-square analysis could not be applied in the last case as only 3 parasitoids selected *P. laxa* on the first day, and not one on any subsequent day.

The results obtained from contingency tables using the GLM, confirmed those of the Chi-square analyses. Choice of host by *T. howardi* was not dependent on the duration of exposure to the hosts in the tests involving *C. partellus* versus *X. stemmator* and *H. armigera* versus *P. laxa*, but was dependent on duration of exposure in comparing *C. partellus* to *H. armigera* and to *P. laxa* (table 1).

TABLE 1

Host preferences of T. howardi *in long term (5 days) preference tests and the change of preference over time*

Options	Host preferred (a)	Overall Odds ratio (U)	P[1]	Day	Hosts chosen (n) out of 120	a from n	Odds ratio/day (relative to day 1)	P[2]
Cp vs Xs	*Cp*	1.3	< 0.20	1	20	14	—	< 0.20
				2	17	9	—	
				3	20	7	—	
				4	21	15	—	
				5	19	11	—	
Ha vs Pl	*Ha*	23.7	< 0.01	1	20	17	—	< 0.01
				2	18	18	—	
				3	8	8	—	
				4	12	12	—	
				5	16	16	—	
Cp vs Pl	*Cp*	3.6	< 0.01	1	16	10	—	< 0.02
				2	14	8	0.7	
				3	16	12	1.5	
				4	21	18	3.0	
				5	16	16	133252.3	
Cp vs Ha	*Cp*	2.1	< 0.05	1	24	9	—	< 0.01
				2	13	10	5.6	
				3	15	12	6.7	
				4	16	12	5.0	
				5	12	11	18.4	

Cp = *C. partellus*, *Xs* = *X. stemmator*, *Ha* = *H. armigera*, *Pl* = *P. laxa*.
[1] The probability refers to the odds ratio of (a) being chosen.
[2] The probability refers to the odds ratio/day; only for *Cp* vs *Pl* and *Cp* vs *Ha* was choice of host dependant on day.

Contingency tests using GLM showed tendencies by *T. howardi* for one of the hosts in all the short term tests, and yet none of these were significant preferences (table 2). Previous experience was observed to influence the parasitoids oviposition tendency but was in no case found to be significant. It has been reported that experience by adult parasitoids often affects subsequent behaviour (Vet & Groenewold, 1990). Even though this phenom-

Table 2
Host preferences of T. howardi *in short term (200 min) preference tests and the influence of experience*

Options	Host preferred (a)	Odds ratio (U)	P*	Experience	Hosts chosen (n)	a from n
Cp vs Xs	*Cp*	1.8	< 0.20	*Cp*	16	13
				Xs	14	9
				none	15	7
Ha vs Pl	*Ha*	21.5	< 0.10	*Ha*	17	17
				Pl	12	12
				none	16	14
Cp vs Pl	*Cp*	2.2	< 0.20	*Cp*	13	10
				Pl	17	10
				none	23	16
Cp vs Ha	*Ha*	2.5	< 0.20	*Cp*	15	10
				Ha	11	8
				none	20	15

Cp = C. partellus, Xs = X; stemmator, Ha = H. armigera, Pl = P. laxa.
* The probability of accepting the odds ratio.

enon was not significant in the short term tests, in the long term tests *T. howardi's* preference for *C. partellus* over *P. laxa* and also over *H. armigera* increased significantly with experience.

Regardless of which host *T. howardi* emerged from, it tended to select *H. armigera* more frequently than *C. partellus* and *P. laxa.* In neither of these cases was there a significant preference, however, there was a large difference in odds ratio in both cases, which indicated that the host from which the parasitoid emerged had an influence on its resultant choice (table 3). A female parasitoid with a wide host range sometimes prefers the host species from which she has been reared (Jackson, 1937; Oghushi, 1960; Vinson, 1976; Eisjackers & Van Lenteren, 1970). Even when there is no attraction for a certain host, this can sometimes be induced by rearing the parasitoid on the host (Thorpe & Jones, 1937). However, it is reported that preadult experience generally has only a minor effect on adult host-searching behaviour, compared to adult experience (Vinson *et al.,* 1977; Sandlan, 1980; Vet, 1983; Drost *et al.,* 1988; Mandeville & Mullens, 1990).

T. howardi is polyphagous, and under laboratory conditions has a very wide host range (Kfir *et al.,* 1993). However, no parasitoid appears to be completely indiscriminate (Doutt, 1959), and under natural conditions will attack only a fraction of the species on which development is actually possible. In the artificial conditions of a laboratory one can remove the barriers which separate potential hosts and parasites in nature.

Although in the laboratory *T. howardi* showed preference for phytophagous over parasitic insects, in the field it is considered unlikely that females searching for hosts and encountering a parasitoid pupa would move elsewhere in search of a lepidopterous host before attacking the parasitoid (Bennett, 1965; Kfir, *et al.,* 1993). Moreover, differences in host searching time were recorded for different hosts (Moore & Kfir, 1995), and this may indicate that less favourable hosts can initially be ignored, the parasitoid searching for a more favourable host. The less favourable host may later be attacked if no more favourable host is found.

TABLE 3

Influence of the host from which T. howardi *emerged on its host preference*

Options	Host emerged from	Hosts chosen (n)	Host preferred (a)	a from n	Odds ratio (U)	P*
Cp vs Ha	*Ha*	46	*Ha*	33	2.5	< 0.2
	Cp	62	*Ha*	32	1.1	> 0.5
Ha vs Pl	*Ha*	45	*Ha*	43	21.5	< 0.1
	Pl	55	*Ha*	34	1.6	< 0.3

Cp = *C. partellus*, *Ha* = *H. armigera*, *Pl* = *P. laxa.*
* The probability of accepting the odds ratio.

INFLUENCE OF HOST AGE ON PREFERENCE

T. howardi showed no preference to any particular age of its hosts. There were no significant differences between numbers of parasitoids ovipositing in different aged hosts, nor between duration of time spent ovipositing in different aged hosts (table 4).

TABLE 4

Influence of host age on the preference of T. howardi

Host	Host age (days)	Parasitoids ovipositing (n)	Mean oviposition time (mins) $\bar{x}$	± SE
Cp	1	33	66.06	4.08
	5	32	68.75	5.38
Ha	1	22	84.54	6.02
	5	24	86.67	5.89

Cp = *C. partellus*, *Ha* = *H. armigera*.

HOST DISCRIMINATION

No correlation was found between previous experience and host discrimination. Therefore previous experience was disregarded in the t-tests. Data were transformed by log (x + 1) as variance was larger than mean with some zero counts (Elliott, 1983). *T. howardi* significantly preferred the just parasitised pupae to the unparasitised pupae (t = −2.96; P = 0.01). *T. howardi* showed no discrimination between pupae parasitised 1 day ago and unparasitised pupae. *T. howardi* significantly preferred unparasitised pupae to pupae parasitised 2 days ago (t = 3.22; P = 0.009), pupae parasitised 5 days ago (t = 8.70; P = 0.000006), and pupae parasitised 12 days ago (t = 9.24; P = 0.000003) (fig. 1).

Host discrimination appears to be common among the parasitic Hymenoptera (Eisjackers & Van Lenteren, 1970; Vinson, 1976). This differentiation may result from an odour left on the host by the parasitoid which first contacts it (Flanders, 1951), or from an injected secretion (Vinson, 1976). However, this is probably unlikely in the case of the gregarious

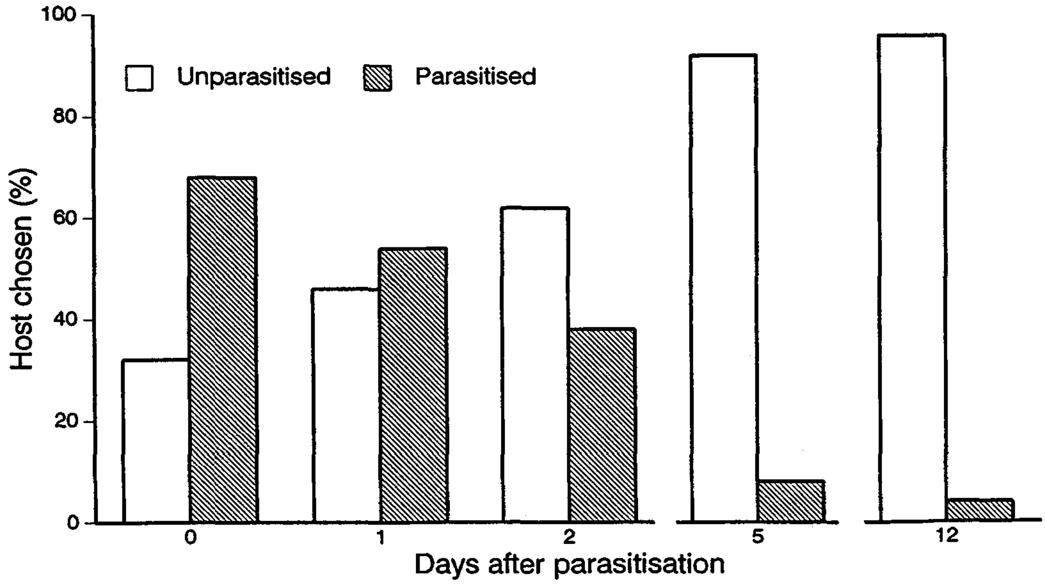

Fig. 1. Discrimination of *T. howardi* between parasitised and unparasitised pupae of *H. armigera*.

T. howardi, as host pupae when placed in the parasitoid cages, are attacked continually and simultaneously by numerous individuals. If such an odour is transferred by the parasitoid to the host it is normally detectable within seconds to minutes (Van Lenteren, 1976), whereas *T. howardi* appears to start discriminating against parasitised hosts only 2 days after initial parasitisation.

A peculiar phenomenon is the apparent preference for parasitised hosts during the first day after parasitisation. No explanation could be found for this.

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RÉSUMÉ

Choix de l'hôte chez l'hyperparasitoïde *Tetrastichus howardi* (Hym. : Eulophidae)

Des expériences en laboratoire ont montré que *Tetrastichus howardi* (Olliff) préfère, comme hôtes, les lépidoptères, *Chilo partellus* (Swinhoe) (Pyralidae) et *Helicoverpa armigera* (Hübner) (Noctuidae) à leurs parasitoïdes respectifs, *Xanthopimpla stemmator* (Thunberg) (Hym. : Ichneumonidae) et *Palexorista laxa* (Curran) (Dipt. : Tachinidae). Si *T. howardi* a déjà parasité auparavant un certain hôte, sa préférence pour cet hôte s'accroît mais pas significativement. Par ailleurs, quand il est élevé sur un hôte donné, sa préférence pour cet hôte augmente. *T. howardi* ne montre par contre aucune préférence pour un stade particulier de son hôte. Il est capable de distinguer un hôte parasité d'un hôte non parasité et s'il préfère au début les hôtes parasités, il montre, au bout de deux jours, une préférence pour ceux qui ne le sont pas.

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