Influence of Feeding Treatment, Host Density, Temperature, and Cool Storage on Attack Rates of *Tachinaephagus zealandicus* (Hymenoptera: Encyrtidae)

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ABSTRACT *Tachinaephagus zealandicus* Ashmead is a gregarious endoparasitoid that attacks third instars of muscid flies, including house flies, *Musca domestica* L. A colony of this parasitoid was established from samples collected from a poultry farm in Santa Cruz da Conceição, São Paulo, Brazil. The objective of this study was to evaluate the influence of feeding treatment, host density and temperature on attack rates on *T. zealandicus*. Parasitoids that were given honey as adults attacked two to three times as many house fly larvae (25 host attacks/female/d) as parasitoids that were given only water or nothing. Host attacks and progeny production by *T. zealandicus* on house fly and Chrysomyia putoria increased over the range of host:parasitoid ratios tested, reaching a maximum of 21–22 hosts killed and 13 progeny produced/female/d at the highest host density of 32 larvae/female. Host attacks were higher at 22°C than at the other temperatures studied (20–29°C), but differences in attack rates were small over the range of 20–27°C (10–13 host attacks/female). Comparatively few hosts (6.3) were attacked at 29°C. Higher rates of progeny production also were observed among parasitoids tested at lower temperatures (9–11 progeny produced/female at 20–22°C) than at 29°C (1.8 progeny/female). Females of *T. zealandicus* that were stored at 15°C after emergence had highest rates of host attacks (58–62 hosts killed per group of five female parasitoids) and progeny production (174–261 progeny) after 6–12 d of storage at this temperature; relatively few hosts were attacked or parasitized (6–9 host attacks and progeny/group) after 0 or 1 d at 15°C.

KEY WORDS *Tachinaephagus zealandicus*, muscid flies, feeding treatment, host density, temperature, parasitoid female age

*Tachinaephagus zealandicus* Ashmead is a gregarious parasitoid that attacks third instars of muscid flies. Silveira et al. 1989 described *T. zealandicus* attacking Cochliomyia hominivorax (Coquerel) (Calliphoridae) and Synthesiomyia nudiseta (Wulp) (Muscidae) in the Brazilian states of Sao Paulo and Minas Gerais, respectively. Costa (1989) found *T. zealandicus* associated with pupae of *Musca domestica* L., Stomoxys calcitrans (L.) and Muscina stabulans (Fallén) (Muscidae) collected in a poultry house located in the interior of Sao Paulo. Monteiro and Pires do Prado (2000) found *T. zealandicus* emerging from pupae of *Musca domestica*, Chrysomyia putoria (Wiedemann), and Muscina stabulans collected in poultry facilities in the interior of Sao Paulo. *T. zealandicus* is a provigenic parasitoid and does not appear to host-feed.

Because of the potential importance of this species as a fly biological control agent in the Southern Hemisphere, a colony of *T. zealandicus* was established in our laboratory in 1998. Studies of the biology of *T. zealandicus* were conducted by Olton and Legner (1974), and Ferreira de Almeida et al. (2002) examined the development time and longevity of this species at six different constant temperatures. Although these studies provided substantial information about these aspects of the biology of *T. zealandicus*, little is known about host attack rates and progeny production by this species under different environmental conditions. This information is needed for developing rearing procedures that will make efficient use of host resources and optimize production and accumulation of vigorous parasitoids for possible releases. The objectives of the current study were to address the following questions. What is the effect of feeding treatment and host species on host attacks and fecundity? What is the effect of temperature and host:parasitoid ratio on host attacks and fecundity? Can parasitoids be held at cool temperatures (15°C) without compromising attack rates and fecundity?

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Materials and Methods

Insect Colonies. *Tachinaephagus zealandicus* were from a colony originally established from samples collected from a poultry farm in Santa Cruz da Conceição, Sao Paulo, Brazil, and had been maintained on *Chrysopa putoria* for 14 generations at the time of testing. Parasitoids were maintained in 2-liter clear plastic boxes covered by snap-on plastic lids with screened openings. Cages were stocked with ~2,000 parasitoids per cage and held at 25 ± 1°C, 60 ± 10% RH, and a photoperiod of 12:12 (L:D) h. Honey and water were provided to the insects and *C. putoria* larvae were exposed to 2-d-old females at a host:parasitoid ratio of 20:1 for four consecutive days. Parasitized pupae were removed from the cages daily and held in a rearing chamber at 22 ± 1°C. *C. putoria* were also from a colony originally established from the poultry farm in Santa Cruz da Conceição. Larvae were reared using the diet described by Leal et al. (1982), and adults were held in cages under the environmental conditions described above for *T. zealandicus*. Flies were given water and sugar ad libitum and periodically given liver for egg maturation and oviposition. *Musca domestica* were from a colony originally established from poultry farms in central Florida in the early 1980s. Larvae were reared on a diet of 50% wheat bran, 30% ground alfalfa, and 20% corn meal plus water, and adults were fed a mixture of powdered milk, sugar, and powdered egg yolk.

Influence of feeding treatment on host attacks and progeny production. One hundred sixty females were placed individually in 100-ml clear plastic cups covered by snap-on plastic lids with screened openings. The parasitoids were less than 6 h old at the time of the experiment and were assumed to have mated (unpublished observations). Females were assigned to four different feeding treatments: treatment I (honey + water); treatment II (only honey); treatment III (only water); and treatment IV (starvation). In addition, the parasitoids were provided with 16 fly larvae for oviposition. Half of the parasitoids were provided with larvae of *M. domestica* and the other half were provided with larvae of *C. putoria* (n = 20 females for each host species and feeding treatment combination). Larvae were removed and replaced with new larvae each day for three days. Larvae that had been exposed to parasitoids were held for fly and parasitoid emergence under the conditions described above. Differences in the number of host attacks (number hosts from which flies did not emerge) and progeny for each feeding treatment were evaluated by analysis of variance (ANOVA), and means were separated using Tukey’s method (P ≤ 0.050) under the general linear models (GLM) procedure of SAS (SAS Institute 1992). Host attack data were not adjusted for control mortality because of the low control mortality in all the tests (0.5–4%).

Influence of host density on host attacks and progeny production. One hundred individual mated females within 24 h of emergence were placed individually in 100-ml clear plastic cups covered by snap-on plastic lids with screened openings. The parasitoids had been provided with water and honey before being removed for the test. Females were provided with five different densities of either *M. domestica* or *C. putoria* larvae: 2, 4, 8, 16, and 32 larvae per female (n = 10 females per host species and density). After 24 h the females were removed and the exposed fly immatures held for fly and parasitoid emergence as before. No food was provided to the females during the exposure to host larvae. Differences in the number of host attacks and progeny production were evaluated by two-way ANOVA using host species, density and host species × density as model effects using the GLM Procedure of SAS (SAS Institute 1992).

Influence of Temperature on Host Attacks and Progeny Production. One hundred individual mated females within 24 h of emergence were placed individually in 100-ml clear plastic cups covered by snap-on plastic lids with screened openings and placed in rearing chambers maintained at either 20, 22, 25, 27, or 30°C (20 females per temperature). The parasitoids were then provided with 30 *C. putoria* larvae each and honey during a 24-h exposure. After exposure, the females were removed and the fly immatures were held at 25°C for fly and parasitoid emergence. Differences in the number of host attacks and progeny for females at each temperature were evaluated by ANOVA, and means separated using Tukey’s method under GLM Procedure of SAS as before (SAS Institute 1992).

Effect of Storage at 15°C on Rates of Host Attacks and Progeny Production. Females were collected from colony cages within several hours of emergence and transferred to a rearing chamber maintained at 15°C. Parasitoids in this cool chamber were provided with water and honey (but not hosts) for 24 d, during which time samples of parasitoids were removed and assessed for host attack rates and fecundity. Five groups of five females each were removed from the chamber on each of days 1, 2, 6, 12, and 24 and provided with *C. putoria* larvae (75 larvae per group of five females) for 24 h at 25 ± 1°C, 60 ± 10% RH. Exposed hosts were removed from the parasitoids after 24 h and held for fly and parasitoid emergence. Differences in the number of killed pupae and progeny production as a function of storage time (days since emergence) at 15°C were evaluated by ANOVA, and means separated using Tukey’s method under the GLM procedure of SAS (P < 0.05) (SAS Institute 1992).

Results

Influence of Feeding Treatment on Host Attacks and Progeny Production. When *M. domestica* larvae were used as hosts, *T. zealandicus* attacked significantly more hosts when honey was included in their diets than when they were either starved or given only water (Table 1). The parasitoids killed about three times more house fly hosts (24.9 hosts killed) when they were given honey and water than when they were given neither (8.4), and about twice as many as when they were given only water (13.1). When *C.
putoria larvae were used as hosts the greatest numbers of fly immatures were killed when the parasitoids were given honey and water (18.9 hosts killed), but this was only significantly different from the treatment where no honey or water were provided (11.4). Progeny production among individuals was more variable than host attacks, and this variation prevented the detection of significant treatment effects (Table 1), however, very few progeny were produced by parasitoids that were starved and exposed to larvae of the house fly. Two-way ANOVAs indicated that the host species (house fly or C. putoria) had no significant effect on overall attack rates or on the production of female progeny by T. zealandicus. Significantly more males emerged from C. putoria than from M. domestica, but there were no significant differences in female emergence from the two fly species (Table 3).

**Influence of Temperature on Host Attacks and Progeny Production.** T. zealandicus females killed the greatest numbers of C. putoria immatures at 22°C (12.6 host attacks per female) and the fewest at 29°C (6.3) (Table 4). Differences in attack rates over the range of 20–27°C were small and not statistically significant. Similarly, progeny production ranged from 6.0 to 10.9 progeny per female in the range of 20–27°C, whereas few progeny were produced (1.8) at the high temperature of 29°C.

**Effect of Storage at 15°C on Rates of Host Attacks and Progeny Production.** When T. zealandicus were stored at 15°C immediately after emergence and as-

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### Table 1. Host attacks and progeny production of T. zealandicus on Musca domestica and Chrysomyia putoria during 3 d of exposure to four feeding treatments

| Feeding treatment       | Hosts killed (mean [SE]) per female | Mean (SE) no. progeny produced per female |
|-------------------------|-------------------------------------|------------------------------------------|
|                         | Females                             | Males                                   | Total          |
| Honey & water           | 24.9 (2.7)a                          | 2.6 (1.1)a                              | 4.1 (1.5)a     |
| Honey only              | 24.6 (2.5)a                          | 6.4 (3.5)a                              | 7.1 (3.8)a     |
| Water only              | 13.1 (2.2)b                          | 6.3 (3.2)a                              | 8.3 (4.0)a     |
| No honey or water       | 8.4 (1.3)b                           | 0.9 (0.5)a                              | 1.4 (0.6)a     |
| ANOVA F                 | 14.00**                             | Test with M. domestica                  |                |
|                         |                                     | Means within columns under the same host subheading followed by the same letter are not significantly different at P = 0.05 using Tukey’s method. |
| Honey & water           | 18.9 (1.9)a                          | 7.5 (2.0)a                              | 11.6 (3.9)a    |
| Honey only              | 16.4 (1.6)ab                         | 5.5 (2.0)a                              | 7.4 (2.5)a     |
| Water only              | 14.6 (1.4)ab                         | 6.9 (2.9)a                              | 9.2 (4.0)a     |
| No honey or water       | 11.4 (1.2)b                          | 6.0 (1.7)a                              | 8.8 (2.6)a     |
| ANOVA F                 | 4.29**                              | Test with C. putoria                     |                |
|                         |                                     | Means within columns under the same host subheading followed by the same letter are not significantly different at P = 0.05 using Tukey’s method. |
| ANOVA F                 | 1.28 NS                              | **0.01; NS, P = 0.05; NS, P > 0.05.**    |                |

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### Table 2. Two-way ANOVA results for effects of feeding treatment, host density (host:parasitoid ratio) and host species on host attacks and progeny production by T. zealandicus

| Source of variation | ANOVA F                  |
|---------------------|--------------------------|
|                     | Hosts killed             | Progeny produced |
|                     | Females                  | Males           |
| Feeding treatment (FT) | 17.58**                | 0.69 NS          | 0.83 NS         |
| Host species (HS)   | 3.20 NS                  | 2.13 NS          | 3.59*           |
| FT × HS             | 4.14**                   | 0.87 NS          | 0.48 NS         |
| Host density (HD)   | 121.6**                  | 7.85**           | 3.75**          |
| Host species (HS)   | 0.01 NS                  | 2.36 NS          | 6.18*           |
| HD × HS             | 0.36 NS                  | 0.90 NS          | 1.29 NS         |

**,** P ≤ 0.01; *, P ≤ 0.05; NS, P > 0.05.
sessed periodically, maximum rates of host attacks (58–62.4 °C. putoria killed per group of five female parasitoids) and progeny production (174–261 progeny per group) were observed among parasitoids assessed after days six and 12 of storage (Table 5). Cold storage for as long as 24 d had only modest effects on attack rates and total progeny production compared with six and 12 d, and no statistically significant differences were observed in the numbers of female progeny produced after 6, 12 or 24 d of storage. comparatively few hosts were attacked or parasitized when parasitoids were tested immediately after emergence or after 1 d of storage at 15°C.

Discussion

The purpose of this study was to evaluate the response of T. zealandicus to feeding treatment, host density and temperature with respect to attack rates and progeny production. T. zealandicus is a provo- vigenic parasitoid that emerges with a full complement of eggs and dies soon after commencing oviposition. Each ovary of a newly emerged adult female contains 12–16 ovarioles, with a variable number of mature oocytes present in the ovarioles (Olton 1971). The abdomens of female parasitoids dissected after a 48-h oviposition period are sunken and nearly devoid of eggs. From laboratory observations we noted that females did not appear to feed on their hosts but fed avidly on honey when this food was offered to them.

Host feeding in parasitic Hymenoptera is related to the need to secure nutrients, especially protein, for the continued production of oocytes. Proovigenic species such as T. zealandicus typically do not host-feed, whereas most adult parasitoids that continue to develop oocytes after emergence (synovigenic species) do engage in this behavior (Jervis and Kidd 1986). Frequent observations (by M.A.F.A.) of oviposition revealed that females of T. zealandicus may either alight on or walk to a prospective host larva. The host is usually mounted in the posterior dorsal region and inspected with the antennae and the tip of the ovipositor. If the host is acceptable, the ovipositor is inserted either inter- or intra-segmentally at a point just beneath the cuticle. The eggs are deposited in 20–45 s or longer, depending on the activity of the larva (Olton 1971). T. zealandicus females are very aggressive and tenacious, and host inspection/oviposition is probably energetically demanding (Olton 1971). This may explain why the availability of a sugar source such as honey promotes greater numbers of host attacks but does not necessarily result in increased progeny production (Table 1). Our feeding treatment experiment indicated that there is no sig-

| Table 3. Host attacks and progeny production by T. zealandicus at different host (M. domestica and C. putoria) densities |
|---|---|---|
| No. hosts provided per female | Hosts killed (mean [SE]) per female | Mean (SE) no. progeny produced per female |
| | Females | Males | Total |
| Tests with M. domestica | | | |
| 2 | 1.9 (0.1) | 1.1 (0.4) | 2.0 (0.7) |
| 4 | 3.5 (0.2) | 1.3 (0.4) | 4.8 (1.5) |
| 8 | 7.8 (0.4) | 3.5 (0.5) | 11.5 (2.5) |
| 16 | 11.9 (0.9) | 3.3 (1.2) | 11.7 (2.8) |
| 32 | 21.7 (1.8) | 3.3 (0.8) | 12.9 (3.2) |
| ANOVA F | 66.15** | 3.69** | 3.72** |
| Tests with C. putoria | | | |
| 2 | 1.9 (0.1) | 0.6 (0.2) | 2.6 (0.9) |
| 4 | 3.4 (0.2) | 1.2 (0.5) | 4.4 (1.4) |
| 8 | 6.3 (0.5) | 1.1 (0.3) | 5.2 (1.2) |
| 16 | 12.8 (1.0) | 1.2 (0.4) | 7.5 (1.4) |
| 32 | 21.0 (2.1) | 2.8 (0.9) | 12.9 (3.0) |
| ANOVA F | 56.47** | 5.49** | 5.23** |

One-way ANOVAs (**, P ≤ 0.01; *, P ≤ 0.05).

Means within columns followed by the same letter are not significantly different at P = 0.01 using Tukey’s method.

| Table 4. Host (C. putoria) attacks and progeny production by T. zealandicus during a 24-h exposure to host larvae at five different temperatures |
|---|---|---|
| Temp, °C | Hosts killed (mean [SE]) per female | Mean (SE) no. progeny produced per female |
| | Females | Males | Total |
| 20 | 11.4 (1.57)ab | 7.5 (1.84)a | 10.9 (2.02)a |
| 22 | 12.6 (1.67)a | 5.5 (1.66)ab | 8.7 (2.21)a |
| 25 | 10.9 (1.61)ab | 4.5 (1.56)ab | 6.0 (2.05)ab |
| 27 | 10.6 (1.25)ab | 3.2 (1.34)ab | 4.8 (1.52)ab |
| 32 | 6.3 (1.19)b | 1.2 (0.38)b | 1.8 (0.79)b |
| ANOVA F | 3.35* | 3.44** | 4.57** |

One-way ANOVA (**, P ≤ 0.01; *, P ≤ 0.05).
significant difference in progeny production when females are given honey, although honey is known to promote longevity in this species (Ferreira de Almeida et al. 2002). According to Lewis et al. (1998), parasitoids periodically have to interrupt host foraging to seek food sources that supply energy for maintenance and locomotion to allow them to survive until hosts are located. Some adult parasitoids feed on host hemolymph or host-associated honeydew, (Jervis and Kidd 1986, Kidd and Jervis 1989) whereas others feed independently of the host on resources such as floral and extrafloral nectaries, honeydew, or pollen (Jervis et al. 1993).

Most parasitoids require food as adults such as nectar, pollen, homopteran honeydew or host hemolymph. In the laboratory, substitutes for these can include diluted honey, cut raisins, and sucrose solutions. When food is not available, energy resources bound up in eggs, fat body or muscle tissue can be converted into usable energy, but the parasitoids may starve before such conversions release necessary quantities of nutrients for immediate metabolic needs (Heimpel and Collier 1996). Studies have shown that the longevity of both sexes and the fecundity of females typically are significantly reduced in the absence of food (Jervis et al. 1992). Females of Spalangia endius Walker, for example, had higher longevity when they were provided with a combination of honey and host (M. domestica) pupae than when they were given only hosts or honey (Arellano and Rueda 1993).

Parasitoids that do not host-feed can be divided into two groups on the basis of their food searching strategies. The first group finds food resources in the same part of the environment as the hosts, such as aphid parasitoids feeding on the honeydew produced by their hosts (Jervis and Kidd 1986). The second group includes those parasitoids that find food resources and hosts in different parts of the environment and feed, for example, on nectar, pollen and extrafloral nectar (Jervis et al. 1993). No information is available on natural food sources of T. zealandicus in the field. Further investigation will be necessary to evaluate the suitability of potential food resources that are available to the parasitoids in poultry facilities such as fermenting spilled poultry feed and cracked hen eggs. Regardless of the natural food preferences of T. zealandicus, these results and those of Ferreira de Almeida et al. (2002) indicate that provision of honey is beneficial for promoting longevity of this species under colony conditions during times when host larvae are not immediately available.

$T. zealandicus$ females killed $\approx 95\%$ of exposed hosts at the low densities of two to four host larvae/female, and killed $65.6-87.5\%$ of hosts at the higher densities of eight through 32 hosts/female (Table 2). The highest attack rates, 21–22 larvae killed per female, were observed at the highest host:parasitoid ratio of 32. From these experiments and others (M.A.F.A. and C.J.G., unpublished data), 20–25 host attacks per day per female appears to be the upper limit for this species. ANOVA results (Table 3) indicated that host density but not host species was important in determining rates of host attacks and production of female progeny, supporting the notion that both $M. domestica$ and $C. putoria$ are suitable hosts for this species. Field data suggest that $T. zealandicus$ is able to search and survive at low host densities in isolated fly breeding situations (Johnston and Tieg 1922). In a related study, we have reported that $T. zealandicus$ is a short-lived species capable of depositing a fixed number of eggs during a short reproductive period, regardless of host density (Ferreira de Almeida et al. 2002). When host densities are low, the parasitoids allocate more eggs among the available hosts, resulting in shortened development times because of accelerated host resource depletion (Olton 1971). There also appears to be a critical minimum number of eggs that must be deposited to result in successful parasitism. Solitary parasitism in this species is uncommon, and the number of parasitoids produced per host varies with host size. We have also observed that when large hosts such as Sarcoptes bullata are lightly parasitized (<5 parasitoid immatures/host larva), the larvae of $T. zealandicus$ grow to very large sizes but fail to complete development to the pupal stage (unpublished data).

Evaluation of temperature effects demonstrated that $T. zealandicus$ was inhibited by temperatures near $30^\circ C$ and that temperature effects were small in the range of $20-27^\circ C$. The modest differences in response of attack rates to temperature were surprising. This somewhat flat nature of the observed temperature response may have been partially due to temperature effects on development of the host larvae during the
24-h exposure period. Differences in attack rates on live dipteran hosts and prey can be partially masked if the host/prey species develops beyond the window of vulnerability to attack during the experiment, as has been observed with both predators and parasitoids of house fly immatures (Geden and Axtell 1988, Geden 1996). Thus, at higher temperatures the host larvae may develop to a stage where they are less prone to parasitism before the parasitoids have attacked as many larvae as they are capable of attacking. Further experimentation with more frequent provisioning of hosts or narrower observation windows would be required to test this hypothesis with T. zealandicus.

The lower threshold of activity for this species has not been established, however we have observed that the parasitoids are sluggish and show negligible interest in host larvae at 15°C (unpublished observations). Geden (1996) observed that other parasitoids that occur sympatrically with T. zealandicus (Spalangia gemina, S. cameroni and Muscidifurax spp.) are more effective near 25°C. M. raptor killed more house fly pupae at 30°C than either S. gemina or S. cameroni. The two Spalangia species had similar attack rates overall, although attack rates of S. gemina were more suppressed by both low and high temperature than were those of S. cameroni. The Spalangia species studied by Geden (1996) were also collected on a dairy farm 15 km from the source population of T. zealandicus in this study. Field observations during 1998 showed that T. zealandicus was most prevalent from August to December at that site, where the maximum daily temperatures during the latter month were about 29°C (Ferreira de Almeida and Pires do Prado 1999, Ferreira de Almeida et al. 2002). Parasitoids in the field may be able to mitigate the apparently inhibitory effects of high ambient air temperatures by foraging in microhabitats with more moderate local environmental conditions.

Although T. zealandicus is ready to oviposit within 24 h of emergence, the results of the experiment on cool-temperature (15°C) storage indicate that the parasitoids can be stored for at least 12 d at 15°C with no appreciable loss of fecundity. From an operational standpoint, this means that parasitoids can be held in this manner if host larvae are not immediately available, allowing the insectary worker time to produce a batch of host larvae from eggs. This may also facilitate the accumulation of large numbers of parasitoids before making field releases.

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