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# Laboratory evaluation of density relationships of the parasitoid, *Spalangia endius* (Hymenoptera: Pteromalidae), with two species of tephritid fruit fly pupal hosts in Thailand

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**ABSTRACT:** Laboratory experiments were performed on the parasitoid, *Spalangia endius* Walker, attacking the fruit fly pupal hosts, *Bactrocera correcta* (Bezzi) and *B. dorsalis* (Hendel), to determine the effects of parasitoid age, pupal age and density of both parasitoids and pupae on attack rates. *Spalangia endius* females attack at peak rates at approximately 3 d of age. The mean numbers of host pupae attacked per female parasitoid were 8.42 ± 0.26 for *B. correcta* and 7.37 ± 0.38 for *B. dorsalis*, for parasitoids aged 1–7 d. The rate of parasitism of *B. dorsalis* declined to below 50% by day 7 of pupal age, but that of *B. correcta* remained high (> 90%). The experiments on varying host density determined that the numbers of pupae parasitized increased with host density, but the percentage parasitism declined, or was inversely density dependent. The results suggested that female *S. endius* exhibited a Type II functional response. The ovipositional behavior of the parasitoid on the two species of pupal hosts was random. In the experiments on variable host (or parasitoid) density, the percentage parasitism in *B. correcta* was significantly higher than that of *B. dorsalis* at all densities (paired *t*-tests, $p < 0.001$). The oviposition efficiency of *S. endius* on *B. correcta* declined with parasitoid density, and can be described by the regression: $A = 0.38 - 0.21 \log P$ ($F = 8.39$, $df = 1,10$, $p < 0.05$, $r^2 = 0.46$) where A represents the area of discovery and P is number of parasitoids searching. However, searching efficiency of *S. endius* on *B. dorsalis* was lower and relatively constant with parasitoid density: $A = 0.18$ ($F = 1.03$, $df = 1,10$, $p = 0.33$, $r^2 = 0.09$). These results suggest that host and parasitoid densities play an important role in the attack rate of the parasitoid, *S. endius* and that it may be more effective in biological control of tephritid fruit fly, *B. correcta* than of *B. dorsalis*.

**KEYWORDS:** *Spalangia endius*, tephritid fruit fly, density, parasitism, biological control

## INTRODUCTION

Fruit flies (Tephritidae) are major insect pests in many regions of the world.[1] They are widely distributed and infest a wide variety of fruits and vegetables. Early attempts to suppress infestations of fruit flies resulted in the use of exotic entomophagous species for biological control.[2,3]

*Spalangia* spp. (Pteromalidae) are pupal parasitoids of various dipteran hosts[4,5,6,7,8] including tephritid fruit flies.[1,9] In Thailand, *S. endius* has been found in mixed infestations of the tephritid fruit flies, *Bactrocera correcta* and *B. dorsalis* (Kitthawee, unpublished). Thus *S. endius* may be considered a potential biological control agent against fruit flies in Thailand.

There have been reports of house fly and pteromalid parasitoid interactions.[10,11] However, information on the relationships between the pteromalid parasitoid, *S. endius*, and its fruit fly hosts is still lacking. The investigation of host-parasitoid interactions may provide useful information for control of fruit flies in Thailand. In this report, we present experimental results on the relationships between *S. endius* and their fruit fly hosts, *B. correcta* and *B. dorsalis*, concerning four aspects: 1) the suitable age of hosts and parasitoids; 2) host preference of *S. endius*; 3) the effects of host density on success of the parasitoids; and 4) the effects of parasitoid density on attack rate at constant host density.

## MATERIALS AND METHODS

### Parasitoid and Hosts

The pteromalid, *S. endius*, was primarily obtained from fruit fly infested fruit of guava growing in Bangkok and reared in the insectary of the Department of Biology, Faculty of Science, Mahidol University. The *S. endius* colony has been maintained on pupae of the fruit flies, *B. correcta* and *B. dorsalis*, which have been reared on bananas under laboratory conditions at 27 ± 2 °C and 70 ± 10 %RH.

### Age Suitability of Fruit Fly Hosts

Seven different aged groups (1–7 d old) of pupal fruit flies were marked by different colors of luminous paint (BioQuip Product, Inc.). Ten fruit fly pupae in each age group were placed in a plastic cage (10 x 10 x 6 cm). Each cage of pupae was exposed to 7 adult female parasitoids aged 3 d for 24 h. Then the parasitoids were removed and the fruit fly pupae were isolated by age group in different containers for about 5 d. The fruit fly pupae were dissected under a stereomicroscope to determine their level of parasitism. The number of parasitized pupae of both *B. correcta* and *B. dorsalis* was analyzed to determine host suitability. This procedure was replicated 3 times for each species of fruit fly.

### Age Suitability of Parasitoid *S. endius*

Four emerging *S. endius* females were placed in a plastic cage (7 x 9.5 x 5 cm) with 40 1-d-old pupal fruit flies. After 24 h, the pupal fruit flies were removed and replaced by a new set of 1-d-old host pupae. This procedure was performed for 7 consecutive days. Upon removal, the pupae were dissected for parasitoids. The data were analyzed for daily parasitism per parasitoid female in relation to parasitoid age. Three replicates were performed for each species of fruit fly.

### Effects of Host Density on Parasitoid Success

Groups of 1-d-old fruit fly pupae were set up in plastic cages (10 x 10 x 6 cm) at densities at 10, 20, 40 and 80 pupae per cage. Four female parasitoids aged 3 d were introduced into each cage and kept under laboratory conditions. After 24 h, the parasitoids were removed from each cage, and the number of fruit fly pupae parasitized was counted and recorded. There were 3 replicates for each fruit fly species and density, for a total of 24 experimental cages.

### Effects of Parasitoid Density on Host Searching

Female parasitoids aged 3 d were set up in plastic cages (7 x 9.5 x 5 cm) at 4 densities, 1, 2, 4 and 8 parasitoids per cage, with each cage containing 40 1-d-old pupal fruit fly hosts. After 24 h, the parasitoids were removed from each cage and the number of non-parasitized fruit flies was recorded. This procedure was replicated 3 times for each fruit fly species.

### Data Analysis

Descriptive statistics [mean ($\overline{X}$) and standard error (SE)] were used to compare the number (or the percentage) of fruit flies parasitized. Mean numbers or percentages of parasitized fruit fly pupae among pupal age groups and parasitoid age groups were compared using one-way analysis of variance (ANOVA). Comparisons of means were also made using the least significant differences (LSD) test. The age suitability of fruit fly hosts and parasitoids was determined. The two-sample t-test was used to compare the differences between the overall mean number (or percentage) of parsitized pupae of *B. correcta* and *B. dorsalis*, to determine the host preference.

For each density of fruit flies (or parasitoids), the average number (or percentage) of pupae parasitized was calculated. The mean number (or percentage) of parasitized pupae of *B. correcta* and *B. dorsalis* was compared using the paired t-test. The relationships between the number (or the percentage) of hosts parasitized and host (or parasitoid) density were evaluated by regression analysis. Variances were compared by using Bartlett's test. For unequal variances, weighted regression was performed by the inverse of variance of the number (or the percentage) of hosts parasitized. A log transformation was performed on data to linearize the relationships. Normality was checked by the Shapiro-Wilk test.

The random oviposition of parasitoids was predicted by using the "random attack model".[12] The model is

$$N_{par} = N(1 - e^{-Enc/N})$$

where $N_{par}$ = the number of hosts parasitized, N = the total number of hosts, and Enc = the total number of encounters that the parasitoids make with the hosts. In order to determine whether the data fitted random oviposition of parasitoids or not, we used the chi-square test for goodness of fit.

Percentage parasitism was defined as the number of fruit fly pupae parasitized divided by the number fruit fly pupae per cage. We investigated the relationship between the percentage parasitism and host density. If positive, we inferred the relationship was density dependent. If the percentage parasitism declined with increasing host density, the relationship was inferred to be inversely density dependent.

The ability of parasitoids to find or attack the hosts may depend not only on host density but also on their ability to find or attack hosts (or the parasitoid's "area of discovery"). The "area of discovery" for each density of parasitoids ovipositing at a constant density of fruit flies was calculated from the formula:[13]

$$A = (1/P)*(\log_e N/S)$$

where A = area of discovery, P = the number of parasitoids searching, N = the number of hosts exposed, and S = the number of hosts not parasitized. A simple linear regression model was tested for the relationship between the area of discovery of *S. endius* and its density. All analyses were performed with Statistix®.[14]

## RESULTS

### Age Suitability of Fruit Fly Pupae

The mean percentage parasitism of *S. endius* varied with age of fruit fly pupae and species. Pupae of *B. correcta* of all ages were attacked by *S. endius* about equally ($F = 0.88$, $df = 6,14$, $p > 0.05$) while pupae of *B. dorsalis* were attacked by *S. endius* at a rate that tended to decline with pupal age ($F = 2.83$, $df = 6,14$, $p < 0.05$) (Table 1). The highest mean percentage parasitism of *B. dorsalis* was on the first day puparium (93.3 ± 6.7%); hence, fruit fly pupae aged 1 d were used later in our experiments. However, the overall mean percentages of parasitism for *B. correcta* and *B. dorsalis* were significantly different in a two-sample *t*-test under unequal variances ($t = 4.17$, $df = 26.70$, $p < 0.001$). The overall mean percentage parasitism for *B. correcta* (93.8 ± 1.8%) was significantly higher than for *B. dorsalis* (74.6 ± 4.2%).

### Age Suitability of Parasitoid, *S. endius*

Results showed that the attack rate of *S. endius* did not vary significantly with parasitoid age group for either *B. correcta* ($F = 1.38$, $df = 6,14$, $p > 0.05$) or *B. dorsalis* ($F = 0.38$, $df = 6,14$, $p > 0.05$). However, 3-d-old *S. endius* attacked pupae at the highest rate: *B. correcta* with an average of 9.42 ±0.46 pupae per female parasitoid and *B. dorsalis* with 8.33 ± 0.74 pupae (Table 2). The overall mean numbers of pupae parasitized per female parasitoid for *B. correcta* and *B. dorsalis* were 8.42 ± 0.26 and 7.37 ± 0.38, respectively. The means were significantly different in a two-sample *t*-test ($t = 2.29$, $df = 40$, $p < 0.05$). These results showed that *S. endius* attacked *B. correcta* at a higher rate than *B. dorsalis*.

### Effects of Pupal Host Density

There were significant effects of pupal host density on the rate of parasitism with *S. endius* density held constant at 4 females. Increase in the density of pupal hosts produced an increase in the number parasitized, but a decrease in percentage parasitism for both *B. correcta* and *B. dorsalis* (Table 3). The range of pupae parasitized per female parasitoid for each host density group (10–80 pupae) was 2.00 ± 0.00 to 10.75 ± 1.39 (*B. correcta*) and 1.42 ± 0.08 to 7.00 ± 0.38 (*B. dorsalis*). Regression analysis indicated that the relationships between pupal host density (N) and the number hosts parasitized ($N_{par}$) were significant for both *B. correcta* ($F = 84.71$, $df = 1,10$, $p < 0.001$, $r^2 = 0.89$) and *B. dorsalis* ($F = 69.63$, $df = 1,10$, $p < 0.001$, $r^2 = 0.87$) (Figs. 1a, 1b).

**Table 1.** Mean (± SE) percentage pupae parasitized at different pupal ages by 3-d-old *S. endius* females.

| Day* | Mean** | % pupae parasitized |
|---|---|---|
| | *B. correcta* | *B. dorsalis* |
| 1 | 96.7 ± 3.3 $^{a}$ | 93.3 ± 6.7 $^{a}$ |
| 2 | 93.3 ± 3.3 $^{a}$ | 81.7 ± 9.7 $^{a}$ |
| 3 | 100.0 ± 0.0 $^{a}$ | 80.3 ± 10.7 $^{a}$ |
| 4 | 90.0 ± 5.8 $^{a}$ | 73.0 ± 6.3 $^{ab}$ |
| 5 | 96.3 ± 3.7 $^{a}$ | 81.7 ± 9.7 $^{a}$ |
| 6 | 86.7 ± 8.8 $^{a}$ | 66.7 ± 8.3 $^{ab}$ |
| 7 | 93.3 ± 3.3 $^{a}$ | 45.8 ± 10.5 $^{b}$ |
| Overall mean | 93.8 ± 1.8 | 74.6 ± 4.2 |

* = Day, age of fruit fly hosts after pupation.

** = Means within a column followed by the same letter are not significantly different (LSD test, $p < 0.05$)

**Table 2.** Mean (± SE) number of 1-d-old fruit fly pupae (n=40) parasitized per *S. endius* females daily for seven days.

| Day* | Mean no. pupae parasitized | |
|---|---|---|
| | *B. correcta* | *B. dorsalis* |
| 1 | 6.92 ± 0.98 | 7.58 ± 0.73 |
| 2 | 8.42 ± 0.22 | 8.17 ± 0.55 |
| 3 | 9.42 ± 0.46 | 8.33 ± 0.74 |
| 4 | 8.33 ± 0.17 | 7.08 ± 0.88 |
| 5 | 8.92 ± 0.42 | 6.92 ± 1.42 |
| 6 | 8.58 ± 0.42 | 7.00 ± 1.18 |
| 7 | 8.33 ± 1.17 | 6.50 ± 1.70 |
| **Overall mean** | **8.42 ± 0.26** | **7.37 ± 0.38** |

* = Day, age of *S. endius* after emergence.

**Table 3.** Mean (± SE) number of fruit fly pupae parasitized after exposure for 24 h to constant *S. endius* density (4 females) at different pupal densities.

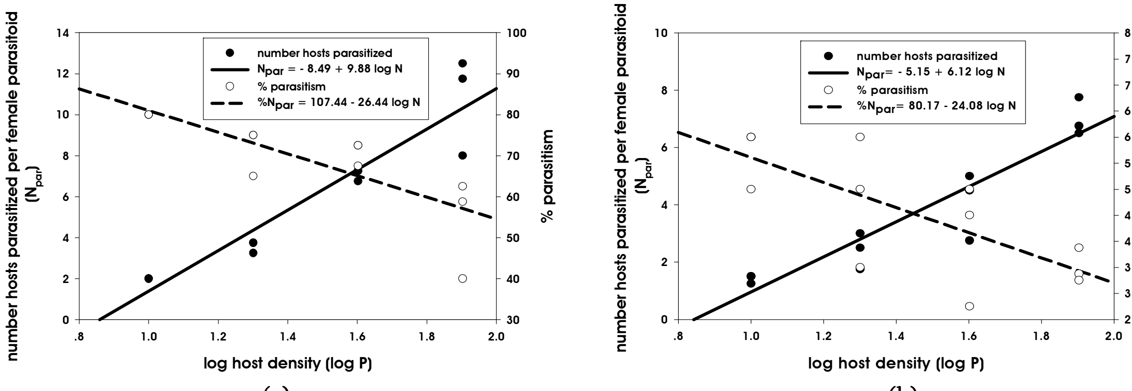
| Host density | Parasitoid: host ratio | Mean no. pupae parasitized per *S. endius* | | Mean % pupae parasitized | |
|---|---|---|---|---|---|
| | | *B. correcta* | *B. dorsalis* | *B. correcta* | *B. dorsalis* |
| 10 | 1:2.5 | 2.00 ± 0.00 | 1.42 ± 0.08 | 80.0 ± 0.0 | 56.7 ± 3.3 |
| 20 | 1:5 | 3.58 ± 0.17 | 2.42 ± 0.36 | 71.7 ± 3.3 | 48.3 ± 7.3 |
| 40 | 1:10 | 7.08 ± 0.17 | 4.08 ± 0.68 | 70.8 ± 1.7 | 40.3 ± 6.8 |
| 80 | 1:20 | 10.75 ± 1.39 | 7.00 ± 0.38 | 53.7 ± 6.9 | 35.0 ± 1.9 |

At low pupal host density, the number parasitized was low, but it increased with increasing host density. Apparently, *S. endius* attacked more pupal hosts when available, suggesting a Type II functional response (Table 3). The ovipositional behavior of *S. endius* at different pupal host densities for *B. correcta* and *B. dorsalis* apparently occurred at random ($\chi^2 = 4.16$, $df = 11$, $p > 0.05$ and $\chi^2 = 4.13$, $df = 11$, $p > 0.05$, respectively) (Table 4).

The percentage parasitism of fruit fly pupae was inversely density dependent. There was a significant decrease in percentage parasitism with increasing pupal host density for both *B. correcta* ($F = 18.41$, $df = 1,10$, $p < 0.005$, $r^2 = 0.65$) and *B. dorsalis* ($F = 11.44$, $df = 1,10$, $p < 0.01$, $r^2 = 0.53$) (Figs. 1a, 1b). The mean percentage parasitism differed significantly between *B. correcta* and *B. dorsalis* (paired *t*-test, $t = 8.18$, $df = 11$, $p < 0.001$) (Table 3).

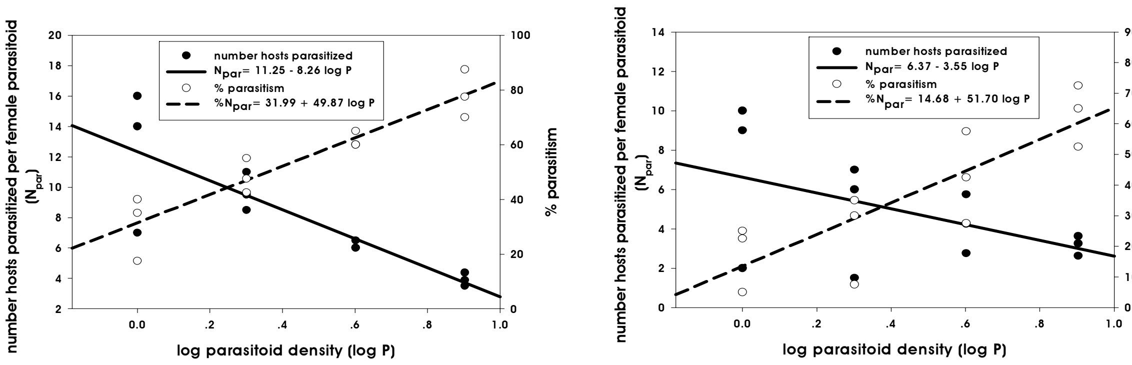
## Effects of Parasitoid Density

The percentage parasitism (%$N_{par}$) increased with



(a) (b)

**Fig. 1.** Relationship between number of hosts parasitized per female parasitoid (left) or percentage parasitism (right), and pupal host density of (a) *B. correcta*, and (b) *B. dorsalis*.



(a) (b)

**Fig. 2.** Relationship between number of hosts parasitized per female parasitoid (left) or percentage parasitism (right), and parasitoid density of (a) *B. correcta* and (b) *B. dorsalis*.

**Table 4.** Mean (± SE) number of fruit fly pupae parasitized per *S. endius* female after fruit fly pupae were exposed for 24 h to constant *S. endius* density (4 females) for different pupal densities compared to the predicted mean.[12]

| Host density | Prasitoid: host ratio | *B. correcta* |  | *B. dorsalis* |  |
|---|---|---|---|---|---|
|  |  | *Observed* | *Predicted** | *Observed* | *Predicted** |
| 10 | 1:2.5 | 2.00 ± 0.00 | 1.63 ± 0.00 | 1.42 ± 0.08 | 1.89 ± 0.04 |
| 20 | 1:5 | 3.58 ± 0.17 | 3.44 ± 0.07 | 2.42 ± 0.36 | 3.95 ± 0.16 |
| 40 | 1:10 | 7.08 ± 0.17 | 6.92 ± 0.07 | 4.08 ± 0.68 | 8.23 ± 0.30 |
| 80 | 1:20 | 10.75 ± 1.39 | 15.33 ± 0.60 | 7.00 ± 0.38 | 16.96 ± 0.17 |

* = random oviposition of parasitoid was calculated from $N_{par} = N(1 - e^{-Enc/N})$
$\chi^2 = 4.16$, $df = 11$, $p > 0.05$ (random oviposition of parasitoid on *B. correcta*)
$\chi^2 = 4.13$, $df = 11$, $p > 0.05$ (random oviposition of parasitoid on *B. dorsalis*)

parasitoid density (P) in both *B. correcta* and *B. dorsalis* (Table 5). The relationship was highly significant in *B. correcta* ($F = 51.16$, $df = 1{,}10$, $p < 0.001$, $r^2 = 0.84$) and in *B. dorsalis* ($F = 34.92$, $df = 1{,}10$, $p < 0.001$, $r^2 = 0.78$) (Figs. 2a, 2b). The mean percentage parasitism in *B. correcta* was significantly higher than that of *B. dorsalis* (paired *t*-test, $t = 5.25$, $df = 11$, $p < 0.001$). The number of fruit fly pupae parasitized per parasitoid, however, was higher at low parasitoid density (Table 5). There was a significant decrease in number of pupae parasitized but increase in pupae parasitized per parasitoid female with increasing parasitoid density for both *B. correcta* ($F = 87.17$, $df = 1{,}10$, $p < 0.001$, $r^2 = 0.89$) and *B. dorsalis* ($F = 5.17$, $df = 1{,}10$, $p < 0.05$, $r^2 = 0.34$) (Figs. 2a, 2b).

The ovipositional efficiency of *S. endius* females can be described by the area of discovery: $A = (1/P)*(\log_e N/S)$. The effect of *S. endius* density on searching efficiency for *B. correcta* can be represented as:

$$A = 0.38 - 0.21 \log P$$

($F = 8.39$, $df = 1{,}10$, $p < 0.05$, $r^2 = 0.46$). When the parasitoid density was increased at constant host density, the area of discovery tended to decrease (Fig. 3).

The relationship between the area of discovery and parasitoid density for *B. dorsalis*, however, was weak ($A = 0.18 - 0.07 \log P$) and not significant ($F = 1.03$, $df = 1{,}10$, $p = 0.33$, $r^2 = 0.09$) (Fig. 3). The area of discovery (A) approximated a constant ($A = 0.18$).

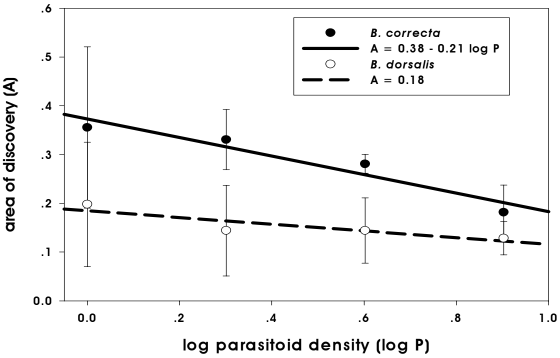


**Fig. 3.** Relationship between area of discovery and parasitoid density.

## DISCUSSION

*Spalangia endius* has been shown to be a solitary pupal parasitoid useful for biological control of several species of flies.[15,16] Based on our results, *S. endius* is a solitary parasitoid of fruit fly (*Bactrocera*) pupae. The host suitability test showed that *S. endius* females positively responded to both *B. correcta* and *B. dorsalis* pupae. They attacked pupae of *B. correcta* of all ages effectively, but attacked younger (aged 1– 3 d) pupae of *B. dorsalis* more than older pupae. A high percentage parasitism has also been reported in various parasitoid host pupae aged 2–3 d.[17,18,19] When they attack old pupal hosts, the host may emerge before the parasitoid eggs hatch. As pupal age had no effect on parasitism of *B. correcta*, *S. endius* may be more effective in controlling natural populations of this species.

Female *S. endius* laid only one egg per pupa in these fruit flies; no superparasitism was observed in this study. On the day of emergence adult females started to oviposit and continued at a constant rate; parasitoid age had no significant effect on the rate of parasitism, although 3-d-old females produced the highest rate of parasitism. The overall mean rate of parasitism in *B. correcta* (8.42 pupae per day) was significantly higher than that of *B. dorsalis* (7.37 pupae per day) suggesting that *S. endius* may be a more effective control agent for the former species.

Host density and parasitoid density are important factors affecting fly mortality and parasitism.[20,21,22] In our experiments, pupal hosts at low density were attacked at a high attack rate which was somewhat inversely density dependent. There was strong competition for hosts and a high percentage of parasitism (Figs. 1a, 1b). At higher pupal host densities, the number of hosts parasitized increased but the percentage parasitized declined. Legner[23] also showed that *S. endius* had a higher attack at higher host density

**Table 5.** Mean (± SE) number of pupae parasitized after 40 fruit fly pupae were exposed to varying densities of *S. endius* females for 24 h.

| Parasitoid density | Parasitoid: host ratio | Mean no. pupae parasitized per *S. endius* | | Mean % pupae parasitized | |
|---|---|---|---|---|---|
| | | *B. correcta* | *B. dorsalis* | *B. correcta* | *B. dorsalis* |
| 8 | 1:5 | 3.92 ± 0.25 | 3.17 ± 0.29 | 78.3 ± 5.1 | 63.3 ± 5.8 |
| 4 | 1:10 | 6.17 0.17 | 4.25 ± 0.87 | 61.7 ± 1.7 | 42.5 ± 8.7 |
| 2 | 1:20 | 9.67 ± 0.73 | 4.83 ± 1.69 | 48.3 ± 3.6 | 24.2 ± 8.5 |
| 1 | 1:40 | 12.33 ± 2.73 | 7.00 ± 2.52 | 30.8 ± 6.8 | 17.5 ± 6.3 |

as a functional response. The rates of parasitism observed support the random attack model[12] (Table 4), with a type II functional response (Table 3). Since the functional response resulted in inversely density-dependent mortality, the parasitoid may be incapable of controlling or regulating the host population by itself.[20,24] However, most biological control programs are intended to inundate the host population, so that a numerical response should result. It may also be possible to obtain a type III functional response under some environmental conditions which would achieve biological control of the fruit fly. Our results call for field trial experiments, and several other factors should be taken into consideration before a conclusion can be made.

In the experiments on variable parasitoid density, the number of pupae parasitized per female parasitoid and the percentage parasitism were similar to those with varying host density. (Tables 3, 5). Increasing parasitoid density did not result in greater numbers of pupae parasitized per female parasitoid. It therefore may be assumed that increased parasitoid density will reduce the response in the parasitoid, *S. endius*. The efficiency of finding or attacking host pupae can be measured by the "area of discovery". Increases in parasitoid density caused an increase in the percentage parasitism but decreases in the area of discovery in *B. correcta*. Our results agree with those described by Hassell and Varley[25] with regard to increase in parasitism being related to decrease in the area of discovery. On the other hand, the area of discovery in *B. dorsalis* was nearly constant at approximately $A = 0.18$, which agrees more closely with Nicholson's assumption that parasitoids would search for their hosts at a constant area of discovery.[26,27]

The data on *B. correcta* suggest that the parasitoid did not lay eggs on already parasitized pupae. If it can discriminate between parasitized and unparasitized host pupae, it should be more useful for biological control against *B. correcta* than *B. dorsalis*. Nonetheless, detailed studies under field conditions are necessary before releasing *S. endius* for control the fruit fly in field populations.

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