Biological Control **23,** 219–227 (2002)
doi:10.1006/bcon.2001.1011, available online at http://www.idealibrary.com on IDEAL®

Performance of Two Fruit Fly (Diptera: Tephritidae) Pupal Parasitoids (*Coptera haywardi* [Hymenoptera: Diapriidae] and *Pachycrepoideus vindemiae* [Hymenoptera: Pteromalidae]) under Different Environmental Soil Conditions

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Received October 12, 2000; accepted October 28, 2001

We evaluated the performance of *Coptera haywardi* (Ogloblin) (Diapriidae) and *Pachycrepoideus vindemiae* (Rondani) (Pteromalidae), both hymenopteran pupal parasitoids of *Anastrepha* spp. (Diptera: Tephritidae). Performance was studied by manipulating the following environmental conditions in the laboratory: (1) soil type, (2) soil moisture content, (3) soil compaction, and (4) depth at which pupae were buried in the soil. There were two experiments: in the first, exposure time of pupae was held constant and in the second, it varied. In the first experiment, *C. haywardi* was significantly more effective than *P. vindemiae* in parasitizing fly pupae. With exposure time held constant (36 h), only soil type and pupal burial depth were significantly related to parasitism rates. While *P. vindemiae* only parasitized pupae located on the soil surface, *C. haywardi* attacked pupae that were buried up to 5 cm deep, performing better in clayey than in loamy soil. In the second experiment, exposure time (24, 36, 48, and 72 h) had no significant effect on parasitism rates, but soil type did. *P. vindemiae* again only attacked pupae on the soil surface while *C. haywardi* was also able to parasitize pupae that were buried up to 5 cm deep. We conclude that *C. haywardi* represents a viable candidate to replace the environmentally unfriendly *P. vindemiae* in augmentative biological control programs against fruit flies.

***Key Words: Coptera haywardi; Pachycrepoideus vindemiae;* pupal burial depth; Tephritidae; parasitoids; biological control; soil type.**

INTRODUCTION

Augmentative biological control of fruit flies (Diptera: Tephritidae) has generally been attempted with larval–pupal parasitoids (Wharton, 1989; Sivinski, 1996). Parasitoid species such as *Diachasmimorpha tryoni* (Cameron) and *D. longicaudata* (Ashmead) (Hymenoptera: Braconidae) have been mass-released to suppress populations of Mediterranean fruit flies (Wong *et al.*, 1991, 1992) and Caribbean fruit flies (Sivinski *et al.*, 1996), respectively. Currently, alternative parasitoid species are being considered as additions to the typical mass-releases of larval–pupal braconids for the control of the Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann), in Mexico and Central America. If combined mass-releases of egg (e.g., *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae), larval–pupal, and particularly pupal parasitoids were attempted, it is possible that flies escaping one form of natural enemy may sucumb to the other (Sivinski, 1996).

Many hymenopterous parasitoids of fruit fly pupae, despite being described early in the 20th century (Silvestri, 1914), have received little subsequent attention. For example, *Dirhinus giffardii* Silvestri (Chalcididae), *Coptera silvestri* (Kieffer) (Diapriidae), *Muscidifurax vorax* Girault (Pteromalidae), and *Pachycrepoideus vindemiae* (Rondani) (Pteromalidae) were introduced from Africa and India to the Hawaiian Islands (Clausen, 1978), but their effect on fruit fly populations has never been seriously evaluated.

Based on the paucity of information on the role of pupal parasitoids in fruit fly ecology and control, our aim in this study was to compare parasitism rates in a native (*Coptera haywardi* (Ogloblin), Hymenoptera: Diapriidae) and an exotic (*P. vindemiae*, Hymenoptera: Pteromalidae) parasitoid species known to attack fly pupae. In an attempt to render the comparison as robust and meaningful as possible from an applied and biological point of view, we evaluated the following factors under controlled experimental conditions: (1) environmental soil conditions (soil type, soil moisture

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1049-9644/02 $35.00

content, and soil compaction), (2) burial depths in the soil where fly pupae were encountered, and (3) exposure time of parasitoids to pupae.

C. haywardi, an endoparasitoid apparently found throughout Latin America (Ovruski *et al.,* 2000), is a specialist species restricted to tephritid pupae such as *Anastrepha striata* (Schiner), *A. fraterculus* (Wiedemann), and *A. ludens* (Loew) (Sivinski *et al.,* 1998; López *et al.,* 1999). Recently, Baeza-Larios *et al.* (2002) also documented successful parasitization of the notorious pest *C. capitata* under seminatural conditions. In contrast, *P. vindemiae* is a generalist ectoparasitoid attacking many species of cycloraphous flies across numerous families and subfamilies, such as *Phormia regina* (Meigen) (Calliphoridae: Chrysomyinae), *Calliphora* sp. (Calliphoridae: Calliphorinae), *Piophila casei* (L.) (Piophilidae), *Musca domestica* (L.) (Muscidae: Muscinae), *Stomoxys calcitrans* (L.), *Haematobia irritans* (both Muscidae: Stomoxynae), *Fannia canicularis* (L.), *F. scalaris* (Fabricius) (Muscidae: Fanniinae), and *Drosophila melanogaster* Meigen (Drosophilidae: Drosophilinae) (Crandell, 1939; Nostvik, 1954; Rueda and Axtell, 1985a,b,c). It has also been reported parasitizing the following fruit fly species (Tephritidae): *C. capitata, Rhagoletis indifferens* Curran, *R. fausta* (Osten Sacken), *A. ludens,* and *A. suspensa* (Loew) (Jiménez-Jiménez, 1967; Clausen, 1978; Rueda and Axtell, 1985a; Burditt and White, 1987). *P. vindemiae* was originally introduced to the American continent from Hawaii in 1955 (Clausen, 1978; Ovruski *et al.,* 2000) and into Mexico from Costa Rica in 1967 (Jiménez-Jiménez, 1967). In Costa Rica it was recently mass-released as a control measure against the Medfly (Camacho, 1992, 1998), raising concerns about the negative impact that thousands of generalist parasitoids could have on the local dipterous entomofauna.

MATERIALS AND METHODS

Study Site

Studies were carried out at the Instituto de Ecología, A.C. in Xalapa, Veracruz, Mexico (19°31′ N. latitude and 96°54′ W. longitude; 1440 m above sea level). Mean annual temperature and rainfall at this site are 19.9°C and 1515 mm, respectively.

Study Insects

Individuals of both *C. haywardi* and *P. vindemiae* used in this study were reared from a laboratory stock of *A. ludens* pupae. On the same day that adult parasitoids emerged, both males and females were transferred to 30 × 30 × 30-cm Plexiglas cages and fed on an *ad libitum* diet of water and honey. Twenty-four hours before the experiment began, groups of five females (4 to 6 days old) were placed in 250-ml plastic containers that included sources of water and honey. Temperature, relative humidity (R.H.), and light regimes in the laboratory were 27 ± 1°C, 60%, and 12:12 (L:D) h, respectively.

Soil Characteristics Tested

Sandy, clayey, and loamy soils collected (respectively) in Jalcomulco, Tejería, and Xalapa, Veracruz were tested. Each soil sample was classified by texture, according to the methods of Bouyoucos (1962), and then sifted and autoclaved before being used. Soil pH values were 6.1, 5.6, and 5.6 for Jalcomulco, Tejería, and Xalapa (sand, clay, and loam), respectively. Each soil type was tested at four moisture levels and under two compaction states. Moisture levels corresponded to 30, 50, 70, and 90% saturation and soil compaction states were either 1 or 0 g/cm^3 (i.e., uncompacted). To obtain the required moisture levels, first we placed a 900-cc soil sample, previously maintained at 30% relative humidity, in a 1-L plastic container and then added water until the desired humidity level was achieved. Moisture content was measured with a potentiometer (Kelway Soil Tester, Type-36).

Experimental Protocol

We performed two sets of experiments. In the first, we determined how parasitism rates by *C. haywardi* and *P. vindemiae* were affected by soil type, soil moisture content, degree of soil compaction, and depth in the soil at which fly pupae were encountered (i.e., burial depth). In the second, we assessed how soil type, depth of pupa in the soil, and length of pupal exposure to female parasitoids affected parasitism rates (percentage of pupae parasitized) in both species.

Experiment 1. The design of the first experiment was a 2 × 3 × 4 × 2 × 6 factorial arrangement of treatments as follows: two parasitoid species (*C. haywardi* and *P. vindemiae*), three soil types (clay, sand, and loam), four soil moisture contents (30, 50, 70, and 90%), two soil compaction states (compacted and uncompacted), and six burial depths of pupae within the soil (0, 1, 2, 3, 5, and 7 cm). This means that there were 288 combinations of treatments. Given that there was a set of 10 pupae for each combination (see below), a total of 2880 pupae were used.

For this experiment we used 288 (144 per parasitoid species) 1-L plastic containers (11.4 cm upper diameter; 9.35 cm lower diameter; 13 cm height) filled with moistened soil to a height of 3, 5, 7, 8, or 10 cm. Subsequently, 10 *A. ludens* pupae (3 days old) were placed in each container and immediately covered with soil to a constant level in all containers (10 cm). This meant, for example, that in the case of burial depth 7 cm, pupae were placed at 3 cm from the bottom and then covered with soil until reaching the 10-cm mark in the container. In all cases, there were 3 cm of free

space between the soil surface and the lid covering the container. Following this, soil was compacted in half of the containers for each treatment. Only the "no burial" treatment (0 cm depth) required that the soil be compacted before depositing the pupae, rather than after. Following this preparation, five adult *C. haywardi* or *P. vindemiae* females, previously isolated for 24 h (see under Study Insects), were released in each of the containers and covered to prevent their escape. Once released, female parasitoids were left in the containers with fly pupae for 36 h. During this time, food (i.e., cotton impregnated with honey and water) was made available at the top of the container. Thirty-six hours after introduction, parasitoids were removed from the containers and pupae recovered. Pupae were then deposited in 250-ml plastic containers with vermiculite and maintained under controlled conditions of temperature and humidity until adults had emerged. Controlled environmental conditions were as follows: 26 ± 1°C, 60% R.H., and 12:12 (L:D) h.

Experiment 2. Based on the results of Experiment 1, we designed another experiment considering soil type, pupal burial depth, and exposure time of *A. ludens* pupae. The latter variable was assessed because we were surprised at the low parasitism levels observed and wanted to determine whether pupal exposure time had anything to do with this finding. The design of the second experiment was a $2 \times 2 \times 3 \times 4$ factorial arrangement of treatments, which included two parasitoid species (*C. haywardi* and *P. vindemiae*), two soil types (sand and loam), three burial depths of pupae within the soil (0, 3, and 5 cm), and four exposure times of pupae to female parasitoids (24, 36, 48, and 72 h). This last factor was incorporated to give female parasitoids more time to locate buried pupae at ≥3 cm of depth. In this experiment, soil moisture was maintained at a constant 30%. We used loam and sand since in Experiment 1 the best performance by *C. haywardi* (the only species that penetrated the soil in search of pupae) was observed in clay and the worst in sand. We therefore wanted to ascertain whether sand was an inadequate substrate for parasitoid searching activities and decided to compare it against the second best substrate (as determined in Experiment 1). As was the case with Experiment 1, we used the same number of pupae (10) and parasitoids (5) per container but, in contrast, used 10 replicates per treatment (in Experiment 1 we only used 1 replicate). There were 48 combinations of treatments with 10 replicates of each. Thus, a total of 4800 pupae were used in this experiment.

Data Analysis

Generalized linear models were employed for the statistical analyses of both experiments. These were fitted using the program Genstat 5 (Genstat Committee, 1995).

Because the raw data were the number of pupae parasitized of a total of 10 available per container, we employed models with a random binomial component and logits as the link function (logistic models). Using these models, the significance of the terms was tested with the G^2 statistic, derived from the deviance estimates from model fitting (which are approximately χ^2 distributed). When there were indications of overdispersion, the test of the model's fit was corrected by dividing the deviance of the factors by the residual deviance. This produced a test statistic with an F distribution. We refer here to the overdispersion concept as described by Aitkin *et al.* (1989). In logistic models, considering overdispersion is important when the variance estimator of the response variable (i.e., residual deviance/degrees of freedom) differs significantly from one.

RESULTS

The most striking result of this study was the marked difference in the depth at which the two parasitoid species searched for pupae in the soil. Specifically, *C. haywardi* was able to effectively parasitize pupae buried in the soil (up to 5 cm), whereas *P. vindemiae* only attacked pupae found on the surface. Thus, no statistical tests were necessary to demonstrate differences between parasitoid species with respect to pupal encounter depth. Taking this fundamental difference in behavior into account, we decided to (1) compare the behavior of the two species at the soil surface (where both species attacked fly pupae) and (2) examine the relationship between pupal depth and parasitism by *C. haywardi.*

Experiment 1

After analyzing and comparing the behavior of both parasitoid species at the soil surface, the model (which had shown tendencies toward overdispersion) was fitted by a stepwise forward procedure. This demonstrated that none of the factors, except species, was significant ($P < 0.001$) (Table 1). Of the 240 pupae exposed in this experiment at the soil surface to each species (total of 480 pupae for both species), *C. haywardi* parasitized them at a rate of 49.2%. This was significantly higher than the 19% parasitism recorded for *P. vindemiae* (binomial test, $P < 0.001$) (Table 1 and Fig. 1).

In the second analysis, parasitism by *C. haywardi* was modeled as a function of burial depth of pupae in the soil, soil type, soil humidity, and soil compaction. The resulting model showed no overdispersion and suggested that the ability of *C. haywardi* to seek out and parasitize buried pupae varied significantly with

TABLE 1

Comparison of the Performance of *Coptera haywardi* and *Pachycrepoideus vindemiae* during Experiment 1, Considering Soil Type (Clay, Sand, and Loam), Humidity Level (30, 50, 70, and 90%), and Level of Compaction (Compacted and Uncompacted) in Pupae Placed on the Soil Surface

Factors	*F*	*df*	*P*
Species	21.421	1/46	<0.001
Soil type	0.417	2/45	0.661
Compaction level	0.130	1/46	0.720
Humidity level	0.394	3/44	0.758

Note. C. haywardi parasitized pupae at significantly higher levels than did *P. vindemiae*, but none of the environmental factors played a significant role in this.

TABLE 2

Performance of *Coptera haywardi* (Experiment 1) When Exposed to Varying Pupal Burial Depths (0, 1, 2, 3, 5, and 7 cm), Soil Types (Clay, Sand, and Loam), Levels of Compaction (Compacted or Uncompacted), and Humidity Level (30, 50, 70, and 90%)

Factors	G^2	*df*	*P*
Pupal burial depth	253.686	5	<0.001
Soil type	11.941	2	0.003
Soil compaction	2.167	1	0.116
Soil humidity	4.617	3	0.202
Interaction of pupal burial depth and soil type	15.414	2	<0.001
Contrast considering soil textures separately or combining the most similar ones (i.e., loamy and clayey soils)	7.671	2	0.006

Note. Pachycrepoideus vindemiae was not considered here because it only parasitized pupae on the soil surface and, under such circumstances, was outperformed by *C. haywardi* (Table 1). Only significant interactions are presented.

soil type ($P < 0.001$, see Table 2 for details on this interaction). In agreement with this, pupal parasitism rates at each burial depth also varied according to soil type (Fig. 2). *C. haywardi* performed the worst in sandy soil, particularly if pupae were buried (Fig. 2). In clayey soil, individuals of this species parasitized pupae at a significantly higher rate and were able to find them at depths of up to 5 cm (Fig. 2). Soil compaction and soil humidity had no significant effect on the ability of *C. haywardi* to parasitize buried pupae ($P = 0.12$ and 0.20, respectively) (Table 2).

Experiment 2

Levels of parasitism on the soil surface were again different between the two parasitoid species. In contrast to Experiment 1, these differences were not significant (Table 3). Specifically, *C. haywardi* attacked 59.3% of the fly pupae on the soil surface and *P. vindemiae* parasitized 54.4% (800 pupae exposed to each species at the soil surface, considering the two soil types and four pupal exposure times) (Fig. 1). But notably, and as in Experiment 1, only *C. haywardi* was able to locate and parasitize buried pupae. In this species, 474 (92.4%) of the total adult emergences ($n = 513$) stemmed from pupae at 0 cm, 20 (3.9%) were recorded at 3 cm, and 19 (3.7%) were recorded at 5 cm. We note that these numbers are independent of soil type and pupal exposure times.

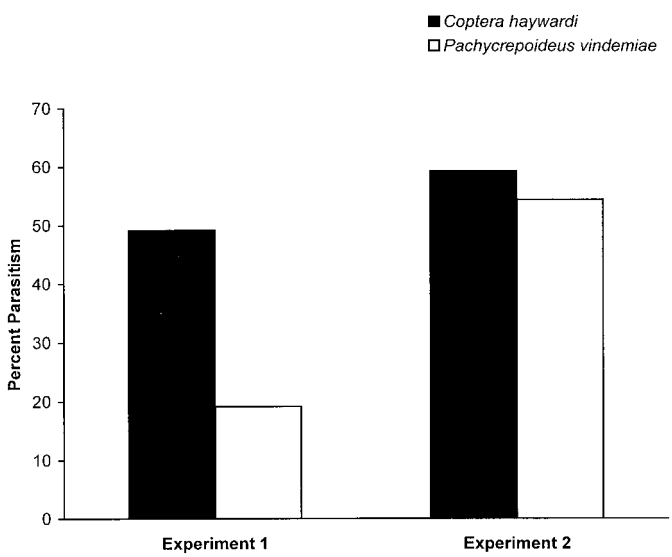

FIG. 1. Parasitism by *Coptera haywardi* and *Pachycrepoideus vindemiae* in pupae placed on the soil surface.

Because the overwhelming majority of emergences in both parasitoid species occurred at the soil surface, parasitism levels were statistically compared between species only in pupae at 0 cm. In this restricted case, the only significant factor affecting parasitism was soil type (Table 3). Both species were significantly more active in loamy soil than in sandy soils ($P = 0.009$). The other two factors under consideration (i.e., species and exposure time) were not significantly associated with parasitism rates (Table 3).

Fitted models for this analysis showed overdispersion. Thus, to test the significance of the various experimental factors, the residual deviation (in this case 2.390) was used, as described under Materials and Methods, to generate an *F* statistic.

In the case of *C. haywardi*, which was capable of parasitizing fly pupae on and below the soil surface, parasitism was modeled as a function of soil depth, soil type, and exposure time. Only soil type, pupal burial depth in the soil, and their interaction were significant ($P < 0.001$ in all cases) and no effect due to exposure time was noted (Table 4). Our modeling procedure indicated that the probability of parasitic activity in sand was high on the surface but almost nonexistent if pu-

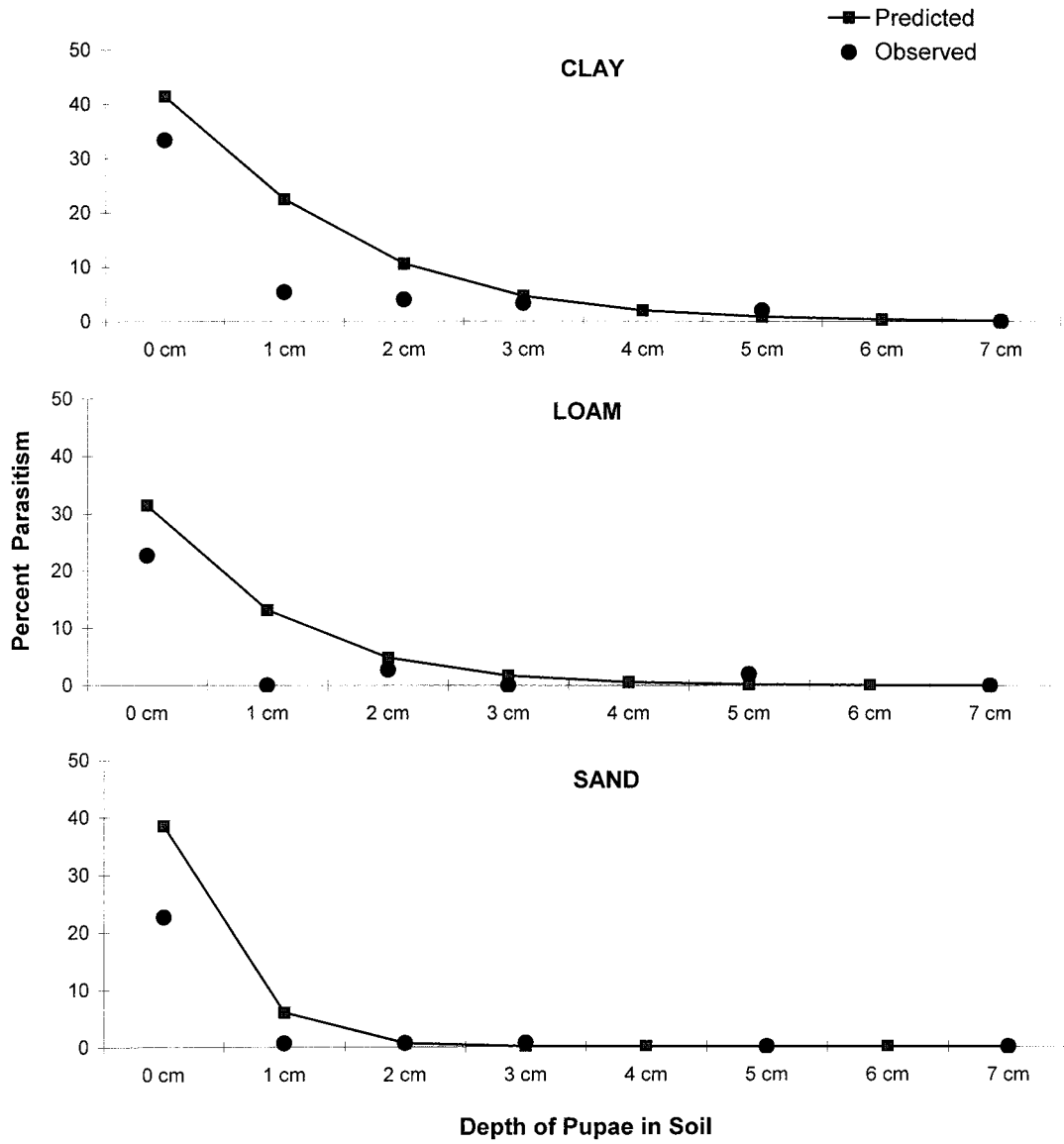

FIG. 2. Parasitism by *Coptera haywardi* with respect to pupal burial depth and soil type (Experiment 1). Observed and modeled (predicted) values are presented.

pae were buried (Fig. 3). Such probability increased, albeit only slightly, in loamy soils (Fig 3).

DISCUSSION

Soil type and pupal burial depth were the two most important factors associated with parasitism by *C. haywardi*. Our findings suggest that overall (i.e., taking into account all factors considered in this study), *C. haywardi* appears to be more effective than *P. vindemiae* at parasitizing *A. ludens* pupae. In addition to parasitizing pupae on the soil surface with an intensity higher than (Experiment 1) or similar to (Experiment 2) that of *P. vindemiae, C. haywardi* also effectively attacked pupae buried at various depths below the surface. In contrast, *P. vindemiae* restricted its activity to the soil surface. The parasitism levels recorded in this study for *C. haywardi* are similar to those reported by López *et al.* (1999) and Baeza-Larios *et al.* (2002) in more natural settings. In addition, Baeza-Larios *et al.* (2002), working with *C. capitata,* reported that successful parasitism and mortality due to unsuccessful parasitoid attack was similar. This implies that the impact of *C. haywardi* on fly populations can be quite high and, in our opinion, that further investigation of the potential of this species becoming part of mass-releases is warranted.

Our finding that *P. vindemiae* was unable to parasitize buried pupae corroborates results from other studies (e.g., Rueda and Axtell, 1985a,b). In contrast,

TABLE 3

Comparison of the Performance of *Coptera haywardi* and *Pachycrepoideus vindemiae* during Experiment 2 Considering Soil Type (Sand and Loam) and Time of Exposure (24, 36, 48, and 72 h) in Pupae Placed Only on the Soil Surface

Factors	*F*	*df*	*P*
Soil type	6.997	1/157	0.009
Species	1.885	1/158	0.172
Exposure time	0.387	3/156	0.762
Interaction of soil type and species	1.060	1/155	0.305

Note. In contrast to Experiment 1 (Table 1), *C. haywardi* did not parasitize pupae at significantly higher levels than *P. vindemiae.* Note that only soil type had a significant effect on levels of parasitism (see text for details).

C. haywardi was able to penetrate the soil surface and parasitize pupae buried as deep as 5 cm. This ability may be reflected in certain physical attributes such as the hypognathus head (Sivinski *et al.* 1998). The ability to dig is of paramount importance if we consider that fruit fly pupae can be buried at depths between 0 and 7.6 cm (AliNiazee, 1974; Ibrahim and Mohamad, 1978; Kasana and AliNiazee, 1996; Hodgson *et al.,* 1998), depending on soil type, compaction, and moisture level (Bressan and Teles, 1990; Eskafi and Fernández, 1990; Salles and Carvalho, 1992; Hennessey, 1994). Importantly, the above-cited studies also determined that most pupae are found at depths of 2 to 3 cm which fall well within the range of parasitic activity exhibited by *C. haywardi* in this study.

Soil type had a significant effect on the ability of *C. haywardi* females to reach and parasitize pupae. In particular, this species performed better in clayey soils than in sands and loams (Experiment 1). This is not surprising, considering that in the habitats where *C. haywardi* is most abundant, clayey soils are also common. Additionally, in Central Veracruz, Mexico, the majority of wild and cultivated fruit trees that host fruit flies (e.g., *Spondias mombin* L., *Citrus sinensis* (L.) Osbeck) are found in areas with clayey soils (Hodgson *et al.,* 1998). Some of the characteristics of clayey soils (e.g., its ability to hold soil moisture for long periods of time) might favor development. Stable moisture levels may be particularly important because *C. haywardi*'s developmental time is relatively long (40–45 days, M. Aluja, unpublished data).

In the case of Experiment 2, in which clayey soil was not tested, both parasitoid species performed better in loamy soil than in sands. This suggests that sandy soil may have presented adverse conditions for adult foraging. Boyce (1934) and more recently Hennessey (1994) speculated that larvae of *Rhagoletis completa* Cresson (walnut husk fly) and *A. suspensa* could not move the high-density soil particles common in loose, sandy soils and, as a result, either pupated on the surface or at very shallow depths. Something similar could be true in the case of parasitoids attempting to burrow in sandy soils.

In Experiment 1, the higher percentage of parasitism noted in *C. haywardi* might also be attributed to its relative specialism (Silvestri, 1914). Being an endoparasitoid (Sivinski *et al.,* 1998), it may possess more intimate relationships with its hosts than in the case of *P. vindemiae.* Thus, it may be more likely to detect specific *Anastrepha* cues than *P. vindemiae,* which may search using generalized cues common to a wide range of potential hosts (e.g., *P. casei, S. calcitrans, M. domestica*) (Rueda and Axtell, 1985a). We note further that in our study the soil covering the pupae was not littered with host fruit which, as speculated by López *et al.* (1999), could be an important cue for foraging *C. haywardi* females. Such cues could perhaps increase patch residence time and search persistence.

Related to the above, we also note that in our study pupae were artificially placed at varying depths in the soil. That is, larvae were not allowed to dig into the soil and pupate. This could explain in part why so relatively few buried pupae were parasitized by *C. haywardi* females. It is conceivable that while digging, larvae leave a trail in the soil that is later used by the female parasitoid to locate pupae (see, however, Baeza-Larios *et al.,* 2002). Because in our study no "larval trail" was present, further work needs to be carried out to ascertain whether this factor could play a role in raising parasitism levels by *C. haywardi* in experimental studies under laboratory conditions.

Finally, we found no statistically significant differences in parasitism rates among the different exposure periods (24, 36, 48, and 72 h). This has important practical implications for the mass-rearing of this parasitoid, because a relatively short exposure period of 24 to 48 h would be sufficient to obtain acceptable rates of parasitism. This information is critical for the establishment of exposure schedules aimed at maximizing production efficiency and lowering costs.

TABLE 4

Performance of *Coptera haywardi* (Experiment 2) When Exposed to Varying Pupal Burial Depths (0, 3, and 5 cm), Exposure Times (24, 36, 48, and 72 h), and Soil Types (Sand and Loam)

Factors	*Df*	G^2	*P*
Pupal burial depth	1017.183	1	<0.001
Exposure time	0.797	3	0.850
Soil type	17.979	1	<0.001
Interaction of pupal burial depth and soil type	10.332	1	<0.001

Note. Pachycrepoideus vindemiae was not considered here because it only parasitized pupae on the soil surface. Only significant interactions are presented. Pupal burial depth was modeled as a continuous variable and therefore degrees of freedom are one.

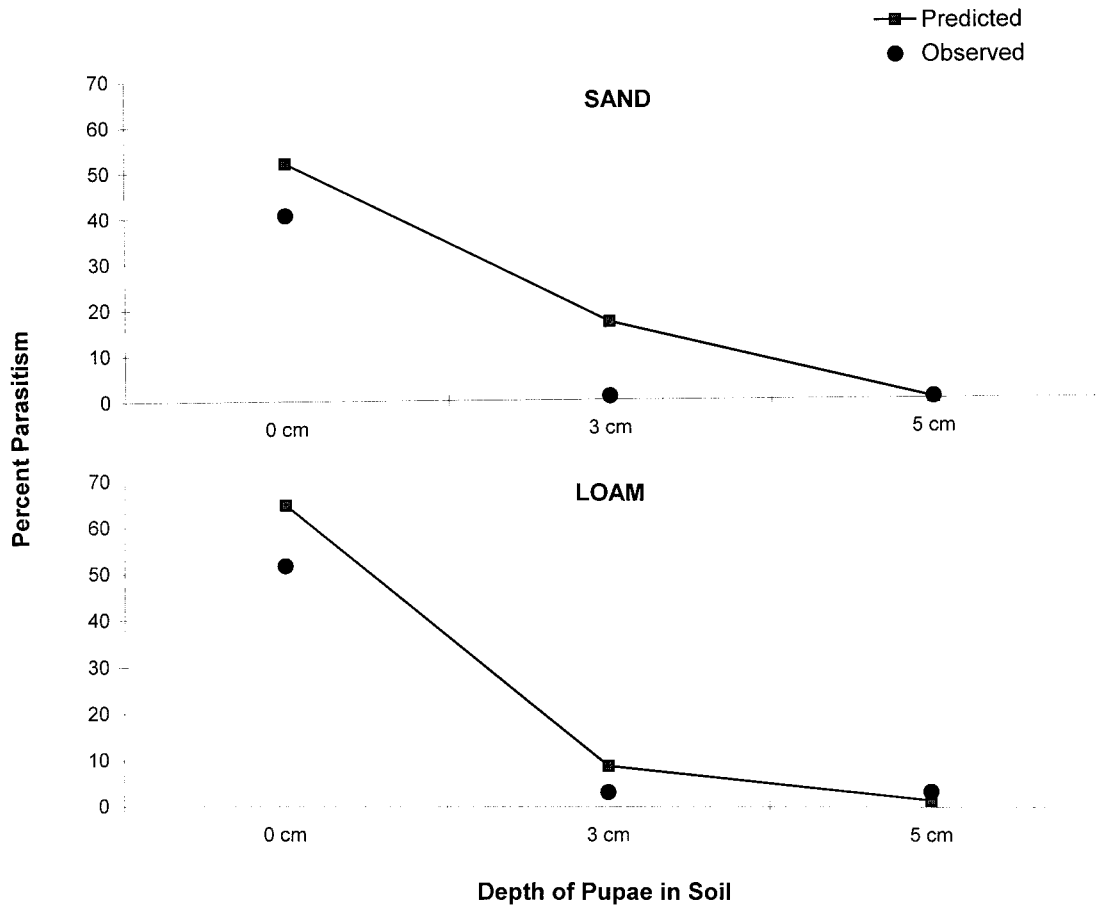

FIG. 3. Performance of *Coptera haywardi* with respect to pupal burial depth and soil type (Experiment 2). Observed and modeled (predicted) values are presented.

Based on the results of this study and a companion paper (Baeza-Larios *et al.*, 2002), we believe that *C. haywardi* qualifies as an alternative to *P. vindemiae* in augmentative fruit fly control programs. First, the environmental impact of localized mass-releases can be safely assumed to be low, given the specialized habits of this endoparasitoid. As noted before, this is not the case with *P. vindemiae,* a species with the potential of negatively impinging on a wide range of nontephritid, native flies (among them critical pollinators). Second, *C. haywardi* has an important advantage over *P. vindemiae* in the sense that it can excavate soil to locate buried pupae and attack pupae on the surface. If recent data documenting that the movement ability of *P. vindemiae* is quite low (Skovgard and Jespersen, 2000) are added, *P. vindemiae* appears to be a poor competitor under field conditions. Third, *C. haywardi* performs well in both clayey and loamy soils (in comparison to sandy soils), which are widespread in fruit- and coffee-producing regions of Latin America. Fourth, and as documented in a companion paper (Baeza-Larios *et al.*, 2002), *C. haywardi* is able to parasitize pupae of *C. capitata* and could, thus, represent a potentially useful addition to the series of techniques applied during eradication efforts of this insect in southern Mexico and Central America, particularly in coffee-growing regions. Fifth, and as also documented by Baeza-Larios *et al.* (2002), *C. haywardi* can kill as many pupae due to unsuccessful attacks as the ones it parasitizes and could thus have a significant impact on local fruit fly populations if mass-released. Sixth, the prospects of rearing *C. haywardi* at a low cost appear good if production schemes are combined with those of other parasitoids (Menezes *et al.*, 1998). On the other hand, *C. haywardi* (at least in Mexico) is restricted to altitudes between 600 and 1000 m above sea level (Sivinski *et al.*, 2000), and other species will need to be found that may be better adapted to hot, tropical climates, such as those occurring between 0 and 500 m above sea level. Additional studies are needed to determine the ability of *C. haywardi* to move within an orchard after being mass-released and its propensity to hyperparasitize pupae already attacked by larval–pupal parasitoids. The latter is particularly important in the case of

multispecies releases because an inability to discriminate parasitized pupae would weaken *C. haywardi*'s effect on pest populations.

ACKNOWLEDGMENTS

We appreciate the generous financial support provided by the Mexican Campaña Nacional contra Moscas de la Fruta (DGSV-SAGARPA-IICA), Sistema de Investigación Regional del Golfo de México (SIGOLFO-CONACyT, Project 96-01-003-V), Comisión para el Conocimiento y Uso de la Biodiversidad (CONABIO, Project H-296), and the U.S. Department of Agriculture (USDA-ARS Cooperative Agreement No. 58-6615-3-025). We are particularly indebted to Jesús Reyes-Flores, former Director General of the Campaña, for his constant encouragement and support. We thank Isabel Jácome and Jaime Piñero for their overall support, Dan Bennack for translating the original manuscript from Spanish to English and for useful comments on scientific content, and Rogelio Macías and Francisco Díaz-Fleischer for critically reviewing an earlier version of this manuscript. Maurilio López discovered *Coptera haywardi* in Veracruz and through this finding made this study possible. Finally, we thank the members of the fruit fly research group at the Instituto de Ecología, A.C. (Gloria Lagunes, Armando Ibañez, Alejandro Vázquez, Braulio Córdova, Diana Pérez, Alberto Jesus, Cecilia Martínez, Emmanuel Herrera, Armando Torres, and Omar Castro) for technical.

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