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Dispersal capacity of fruit fly parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) in irrigated coffee plantations

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ABSTRACT: *Diachasmimorpha longicaudata* is an Old World parasitoid of tephritid fruit flies that was widely introduced in the Americas to control pest species such as the Mediterranean fruit fly *Ceratitis capitata*. Augmentative releases in irrigated coffee plantations in semiarid regions of Brazil are under consideration and dispersal capacity of *D. longicaudata* in this habitat are important to develop release strategies. Approximately 2,000 individuals of *D. longicaudata* (5 to 7 days old) were released in the center of a fruiting coffee plantation every two weeks from Dec. 2009 to Apr. 2010. Dispersal from the central release point was monitored to the north, south, east, west, northeast, northwest, southeast and southwest at 11 distances, beginning at 4.6 m and ending at 90 m from the release point. At each point, a parasitism unit (approximately 120 larvae of *C. capitata* in the 3rd instar wrapped in voile fabric) and 10 coffee beans were collected. The average dispersion distance and dispersion area were estimated by the model proposed by Dobzhansky and Wright (1943). The average dispersion distances were 27.06 m (as estimated by fruit collection) and 33.11 m (as estimated by oviposition traps). The average dispersion areas were 1,315.25 m^2 and 1,752.45 m^2 originating from the collection of beans and parasitism units, respectively. Cohorts of 2,000 adult *D. longicaudata* released at six points ha^{-1} are estimated to result in sufficient colonization to exert significant control of *Ceratitis capitata*.
Keywords: *Ceratitis capitata*, parasitism, average distance of dispersion area, dispersion area

Introduction

The success of augmentative biological control depends upon the ability of released parasitoids to disperse and locate adult foods, shelter, and hosts (Paranhos et al., 2007). The term dispersion can be used to designate the diffusion or migration of individuals of a population or it may be related to the spatial distribution of individuals in a population at a given time (Okubo, 1980; Kareiva, 1986; Turchin, 1989). Movement within an environment can be influenced by plant architecture, height, spacing and phenological state (Gontijo et al., 2010). Thus, the nature of the vegetative habitat and its effect on natural enemy dispersal must be considered when determining the numbers of adults to be released and how and when these releases are performed (Zachrisson and Parra, 1998).

The Asian *Diachasmimorpha longicaudata* (Ashmead) is the most widely introduced Opiinae tephritid fruit fly parasitoid and is arguably the most studied and argumentatively released parasitoid of fruit flies for the control of *Ceratitis capitata* (Paranhos et al., 2008) and *Anastrepha* spp. flies (Montoya et al., 2000; Sivinski et al., 1996). *D. longicaudata* is a larval-prepupal parasitoid that performs best when provided hosts in late 2nd and early 3rd instars. It is relatively simple to mass rear and it forages on fruit on trees and on the ground (Purcell et al., 1994; Sivinski et al., 1998).

Nevertheless, only little information is available on the behavior of *D. longicaudata* in Brazilian agricultural habitats. Therefore, a successful method for local augmentative release, e.g., density of release points and number of parasitoids to be released, is yet to be formulated. Dispersal, survival and parasitism studies are particularly important when they occur in environments considered to have marginal suitability for *D. longicaudata* (Paranhos et al., 2007). One such environment is coffee (*Coffea arabica*) plantations in the hot and dry regions of the northern Minas Gerais, Brazil, which is infested with the Mediterranean fruit fly *Ceratitis capitata*. Coffee is a habitat of concern as it serves as a reservoir for fruit fly populations (Camargos et al., 2015).

In the present study, we tested dispersal by measuring *D. longicaudata* movement from a central release point in a coffee plantation. We estimated the dispersal capacity, seasonal changes in parasitism rates and ultimately recommend the best procedures for augmentative releases.

Materials and Methods

Field experiments were carried out during five months (Dec 2009 to Apr 2010) in Jaíba, Minas Gerais, Brazil (15° 10' 40,1" S and 43° 59' 20,8" W, 484 m elevation), in two hectares with irrigated plantation of Catuaí Vermelho coffee variety.Throughout the study period, no pesticides were sprayed for fruit fly control and no individuals of *D. longicaudata* were released prior to the experiments. The local climate is considered tropical semiarid (Koppen classification) and is characterized by dry winters. The average temperature in the region is 24 °C, with a mean elevation of 500 m and an average annual precipitation of 871 mm (Silva et al., 2012).

The *D. longicaudata* used in the experiments were reared using 3rd stage larvae of *C. capitata* as hosts. Adults parasitoids were kept in wooden framed cages (30 × 30 × 40 cm), covered with organdy mesh, containing approximately 1,000 individuals (sex ratio 1:3, males: females). The adults were provided with water and artificial food source based on honey and water.

Starting from the center of the experimental area, points in the coffee plantation were marked, radiating in the four cardinal directions (north, south, east, and west) and four collateral directions (northeast, northwest, southeast, and southwest). The points were chosen according to plants distribution in the coffee plantation and dictated by spacing between the rows and area. Eleven circles were marked, with radiuses of 4.6, 10, 18, 25, 33, 41, 49, 56, 64, 72, and 90 m, and one point in each direction or eight points per circle, except for the first and last circles, which comprised only four points, totaling 80 points (Figure 1).

Approximately 2,000 parasitoids (1:3, males:females) were released in the center of the marked area at two-week intervals throughout the coffee fruiting period of Dec. 2009 to Apr. 2010, totaling eight releases. The parasitoids were five to seven days old and within their period of maximum fecundity (López et al., 2009).

In order to estimate the dispersal of *D. longicaudata* in the field, a parasitism unit was placed at each marked sampling-point. These parasitism units consisted of about 120 larvae of *C. capitata* in the 3rd instar and artificial food source wrapped in voile fabric, with the dimensions simulating the volume of an infested fruit (Figure 2). The use of traps such as these parasitism units containing larva plus diet attracts parasitoids, reducing the dilution effect of the area, that is, it facilitates to reach the farthest points in the outer circles of the dispersal area (Mills et al., 2006).

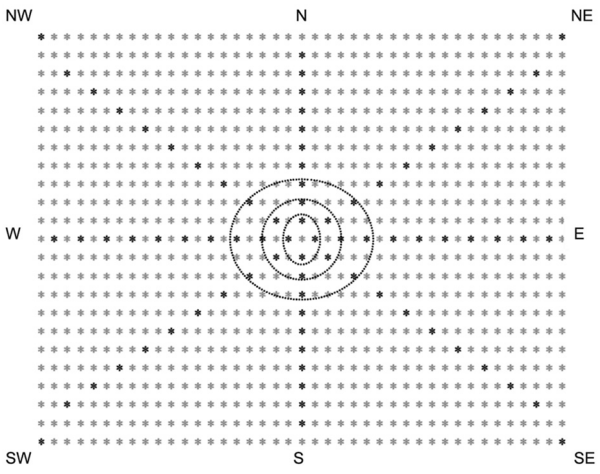

Figure 1 – Distribution design of assessment points of dispersion capacity of *Diachasmimorpha longicaudata* in a coffee plantation. From 11 circumferences, only three were represented for illustration purposes.

The parasitism units were hung on coffee trees at a height between 1.0 and 1.3 m from ground level. Parasitism units were placed at each sample point, totaling eight units per circle, with four parasitism units in the first and last circle, so that each cardinal and collateral direction had ten parasitism units (Figure 1). The parasitism units were deployed for 24 h each, before they were replaced with a new parasitism unit that remained deployed for another 24 h. Thus, samples were taken 24 h and 48 h after parasitoid release to ensure that the parasitism rate was not cumulative. The larvae removed from the units were put in 200 mL plastic cups containing a moist vermiculite layer and covered with voile fabric in order to pupate. Containers were identified by date, location (direction and point) and stored in the laboratory, where they remained under temperature controlled conditions (27 ± 1 °C). After emergence, adult flies and parasitoids were preserved in 70 % ethanol and held in collection at Janaúba, MG, Brazil.

Ten mature coffee fruits were randomly collected from the trees canopy at the previously mentioned sample sites. Four collections (Mar 3 and 24, 2010 and Apr 7 and 21, 2010) were carried out in all 80 sampling points 24 h after the parasitoid release. The fruits were put in 200 mL plastic cups containing moist vermiculite, covered with voile fabric and kept in the laboratory at a controlled temperature 27 ± 1 °C. After ten days, pupae from the vermiculite were screened and fruit pulps were examined carefully. The larvae and the puparia were counted and transferred to glass containers containing vermiculite and covered with voile fabric. Adult insects were preserved in 70 % ethanol and kept in the authors' collection until identification.

Fruit infestation level (I) was calculated as the mean number of puparia per fruit. Parasitism rate (%P) was calculated for each sample in each collection (both for parasitism units and for fruit collections).

%P = [number of adults of parasitoid *D. longicaudata* emerged / total number of adults (*D. longicaudata* and fruit flies) emerged] × 100

A relationship between dispersal (distance from the center to the marked points) and parasitism (24 and 48 h after the release) was calculated through the Pearson correlation (r) and linear regression analyses (SAS-Statistical Analysis System, version 9).

Figure 2 – Parasitism unit in coffee plant.

The average distance of dispersion (DM) and the dispersal area (S^2) of the parasitoid in the plantation, for each collection (evaluation), were estimated by the model proposed by Dobzhansky and Wright (1943) described below:

$$S^2 = [\Sigma(r^3 \times i/a)/\Sigma(r \times i/a) + C/2\pi]; DM = [\Sigma(r^2 \times i/a)/\Sigma(r \times i) + C/2\pi)]$$

where: S^2 (m^2) = dispersion area (m^2) during the experimental period; DM(m) = average dispersion distance (m) of parasitoids during the experimental period; r = distance (m) from the center to the traps (parasitism units or fruit collection points); a = the number of traps per circle (four for the first and last circles and eight for the other circles, at the distances (radius) studied); C = average parasitoids recaptured in the central circle; i = parasitism rate (parasitism units and fruits) in each circle.

In order to relate the dispersal area (S^2) and the average dispersion distance (DM) of the parasitoids to local weather factors (temperature, precipitation, wind speed and relative air humidity), the data were analyzed by the Pearson correlation (r) and linear regression. The monthly average values of climate data were obtained in a Climatological Station in Jaíba, Minas Gerais State, Brazil, about 5 Km from the experimental area.

Results

During the trial period, the average monthly precipitation was 13.9 mm, the average temperature was 25.5 °C and the mean relative humidity was 71 %.

In previous samples of fruit collected between March and June 2009, before the releases of *D. longicaudata*, the average infestation rate of fruit flies in coffee beans was 194.2 pupae kg^{-1} and 0.2 pupae per fruit. We registered 615 adults emerged from the coffee fruit (614 *Ceratitis capitata* and only one parasitoid *Doryctobracon areolatus* (Szépligeti) (Hymenoptera: Braconidae)). No individuals of *D. longicaudata* were collected during these preliminary surveys (Camargos et al., 2015). Therefore, we assume that all individuals of *D. longicaudata* recovered in our study either from fruit samples or in our parasitism units originated from the augmentative releases performed as part of this experiment.

No native parasitoid species were recorded emerging from the fruit samples or from the parasitism units after the experimental releases. Twenty adults of *D. longicaudata* emerged from the beans collected 24 h after the releases and 679 fruit flies, being 677 *C. capitata* (356 females and 321 males) and two males of *Anastrepha* sp. Parasitoids were recovered from coffee beans after the four releases. The average distance estimated in which *D. longicaudata* parasitized on *C. capitata* in the fruit was 27.06 m from the release site and the average area occupied by the parasitoid following release of 2,000 individuals was estimated at 1,315.25 m^2 (Table 1).

Table 1 – Infestation of fruit flies (pupae/fruit), parasitism (%), average distance (DM) and dispersal area (S^2) of parasitoid *D. longicaudata* in fruit samples (collected 24 h after releases).

Release date	Infestation	Parasitism	DM	S^2
		%	m	
3/2/2010	0.4052	4.86	40.23	2,132.9
3/23/2010	0.0012	5.12	13.81	264.78
4/6/2010	0.0187	1.20	4.44	20.46
4/20/2010	0.0175	1.27	49.78	2,842.86

The parasitism units were collected 24 h and 48 h after the release. The parasitism rate of *D. longicaudata* varied among releases and distances from the release point (Table 2). The highest parasitism rate (45 %) occurred in the second radius (10 m far from the center release point) and the lowest (0 %) was obtained in seven out of 16 evaluations in different points on different dates, however, there was no pattern.

Based on the model of Dobzhansky and Wright (1943) and the larvae obtained from the array of parasitism units, *D. longicaudata* infested larvae occurred up to a maximum distance of 76.12 m from the center release point and occupied a maximum dispersion area of 6,368.57m^2 after only 24 h from the release time (Table 3). The highest average parasitism rate (19 %) occurred after 48 h. The average distance of parasitoid dispersal was 35.78 m after 24 h and average dispersion areas were 2217.55 and 1287.35 m^2 after 24 h and 48 h, respectively (Table 3). Parasitism was negatively related to distance (r = 0.80, 24 h after release; r = 0.90, 48 h after release) from the release-site (Table 4), although some parasitism occurred at the farthest sampling distance of 90 m (Figures 3A and 3B). No significant correlations were observed between the average distance of dispersal estimated DM (m) and the estimated colonized area S^2 (m^2) or any abiotic factors (precipitation, temperature, wind speed and relative air humidity) (Table 5).

Discussion

We did not recover any native parasitoid during this study. Although we obtained one individual of *Doryctobracon areolatus*, parasitism of flies found on the coffee beans was close to zero before the release of *D. longicaudata* (Camargos et al., 2015). A similar condition was observed in domestic and commercial orchards in the same region (Alvarenga et al., 2009). However, coffee cultivation in the region is a relatively recent development (the first planting report is from the year 2001) and the first study on natural predators and parasites associated with coffee-pest fly species was carried out by Camargos et al. (2015).

Twenty four hours after release, *D. longicaudata* parasitized medfly larvae in coffee beans at an average distance of up to 49.78 m from the release points and occupied an area of up to 2,842.86 m^2 (Table 1). This is in contrast to a previous release of *D. longicaudata* in a commercial guava orchard where, after 24 h, parasitoids

Table 2 – Parasitism rate of *D. longicaudata* in *C. capitata* larvae placed in parasitism units at different distances (radius) from release points (for 24 (a) and 48 (b) hours after releases).

Release date		Distance from release (m)											
		4.6	10	18	25	33	41	49	56	64	72	90	Average
													%
12/22/2009	a	0.83	17.18	12.29	16.66	5.20	5.62	8.12	2.70	5.10	4.16	0.83	7.15
	b	18.95	44.79	27.39	20.20	23.33	21.97	21.14	9.58	9.37	4.16	0.83	18.33
01/05/2010	a	6.87	10.0	7.08	5.10	2.70	5.41	2.60	2.91	1.77	1.25	2.50	4.38
	b	6.66	8.95	6.97	8.33	4.58	3.02	2.60	1.56	0.10	1.35	0.20	4.02
01/20/2010	a	0	2.29	0.72	0.31	0	0.62	0	0.31	0	1.04	1.66	0.63
	b	13.75	16.66	3.54	4.47	1.97	1.14	1.45	1.04	0.72	1.97	1.45	4.37
02/02/2010	a	0	0.10	0	0.10	0	0	0	0	0	0	0	0.01
	b	0	0.93	0.20	0.52	0.52	0	0	0	0	0	0	0.19
03/02/2010	a	20.41	37.18	21.45	24.06	16.25	9.47	20.00	10.41	10.10	8.64	2.50	16.40
	b	12.5	9.58	9.06	1.77	0.93	2.70	0.93	0.31	0.10	1.56	0.20	3.60
03/23/2010	a	3.75	5.52	3.43	2.91	0.10	1.56	0	0	0	0	0	1.57
	b	3.95	2.70	2.70	1.87	0.72	0	0	0	0	0	0	1.08
04/06/2010	a	12.70	12.29	0.83	1.14	0.52	0.10	1.14	0	0	0.10	1.87	2.79
	b	0.41	0.52	0.10	0	0	0.20	0	0	0	0.10	0	0.12
04/20/2010	a	1.45	5.31	0.41	0.83	0.10	0.72	0.10	0.10	0.14	0	0	0.83
	b	2.08	1.35	0.72	0	0	0	0	0	0	0	0	0.37
% Average	a	5.75	11.23	5.77	6.38	3.10	2.93	3.99	2.05	2.13	1.89	1.17	
	b	7.28	10.68	6.33	4.64	4.0	3.62	3.26	1.56	1.28	1.14	0.33	

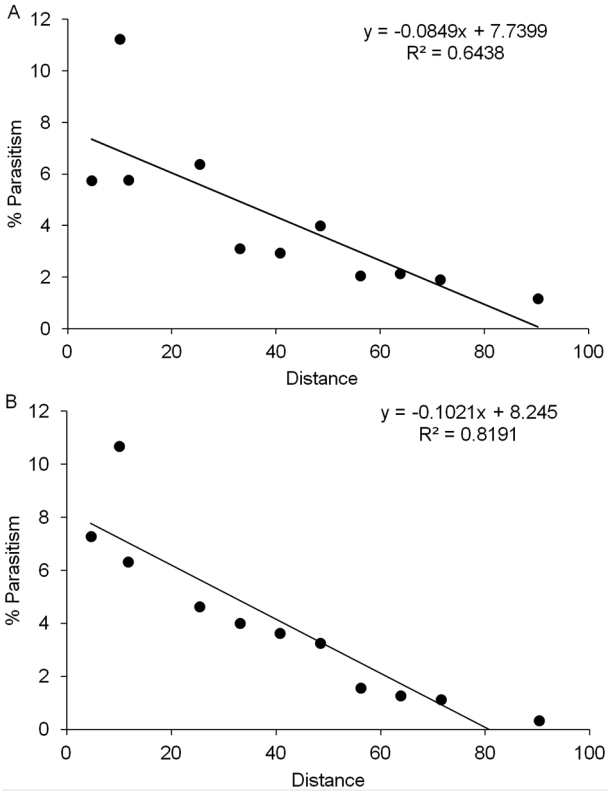

Figure 3 – Average parasitism rate (non-cumulative parasitism rate) by *D. longicaudata* in *C. capitata* larvae placed in parasitism units located in different distances (radius) from the release point in an irrigated coffee plantation, Brazil. A) Average parasitism rate after 24 h of parasitoids release. B) Average parasitism rate after 48 h of parasitoids release.

had attacked larvae at distances of only 20 m (Leal et al., 2008). In part, this difference may be due to the larger sample size of coffee fruits and to certain characteristics of the host plant, e.g., volatility of aromatic compounds. For example, different levels of parasitism can be obtained in the same host in different cultures and, in some cases, parasitoids are more specific in relation to the habitat than to hosts (Ables et al., 1980; Andow and Prokrym, 1991).

In general, parasitism was lower than typically found in field studies. *D. longicaudata* prefers to parasitize host larvae infesting fruit on the ground (Haramoto and Bess, 1970; Sivinski et al., 1997). Silva et al. (2007) observed that *D. longicaudata* shows preference to visit rotten guavas than ripe ones. Segura et al. (2012) showed that oranges previously infested with *C. capitata*, without the presence of larva, were more attractive to females of *D. longicaudata* than non-infested fruits. The authors also concluded that rotten fruits, even when not infested with fruit flies, attracted female parasitoids more than ripe fruits. This suggests that the females use volatile compounds indirectly associated with *C. capitata* larvae. When infested, fruits become rotten more quickly than non-infested ones and, according to Segura et al. (2012), volatiles released by rotten fruits would suggest a higher infestation probability than the ripe fruit itself. If coffee beans are collected at a more advanced maturation stage, i.e., when they have already fallen to the ground, this could result in a larger number of parasitoids recovered as the compounds released by rotten fruits could guide females to the location from further afield, with higher probability of finding the host in infested fruits. In this study, coffee beans were collected only from the canopy of trees after releases.

Table 3 – Average parasitism rate after 24 and 48 hours of releases, average distance (DM) and dispersal area (S^2) reached by parasitoid *D. longicaudata* estimated during the study period, using parasitism units containing *C. capitata* larvae in an irrigated coffee plantation, in Jaíba - Minas Gerais. (Dec. 2009 through Apr. 2010).

Release date	Average percentage	DM	S^2
	%	m	m^2
12/23/09 (24 h)	7.79	45.74	2,517.59
12/24/09 (48 h)	19.18	39.09	1,962.64
1/6/10 (24 h)	4.35	17.93	1,218.82
1/7/10 (48 h)	4.09	33.24	1,599.35
1/21/10 (24 h)	0.61	76.12	6,368.57
1/22/10 (48 h)	4.06	39.25	2,673.54
2/3/10 (24 h)	0.02	21.01	489.63
2/4/10 (48 h)	0.21	24.48	677.98
3/3/10 (24 h)	16.90	43.99	2,539.45
3/4/10 (48 h)	3.00	26.78	1,412.37
3/24/10 (24 h)	1.54	18.27	523.01
3/25/10 (48 h)	1.00	13.68	313.45
4/7/10 (24 h)	2.34	41.46	3,325.95
4/8/10 (48 h)	0.11	29.19	1,584.99
4/21/10 (24 h)	0.94	21.79	757.37
4/22/10 (48 h)	0.31	5.82	74.51
Average 24 h	-	35.78	2,217.55
Average 48 h		26.44	1,287.35

Table 4 – Pearson correlation (r) between the distance (m) where parasitism units were installed and the parasitism rate 24 h and 48 h after release of *D. longicaudata* in irrigated coffee plantation.

Interactions	Pearson correlation coefficient (r)	Correlation
Parasitism × distance (24 h)	0.80	Strong
Parasitism × distance (48 h)	0.90	Strong

Values 0.70 upward or downward indicate a strong correlation. From 0.30 to 0.7 positive or negative indicate mild correlation and 0 to 0.30 means poor correlation.

Table 5 – Pearson correlation (r) between each of the abiotic factors (relative humidity, temperature, wind speed and precipitation) and the variables average distance of dispersion DM (m) or dispersal area S^2 (m^2) of *D. longicaudata* after release in an irrigated coffee plantation.

Interactions	Pearson correlation coefficient (r)	Correlation
Relative humidity × DM	0.13	Poor
Relative humidity × S^2	0.16	Poor
Temperature × DM	0.17	Poor
Temperature × S^2	-0.07	Poor
Wind speed × DM	-0.35	Mild
Wind speed × S^2	-0.36	Mild
Precipitation × DM	0.35	Mild
Precipitation × S^2	0.15	Poor

Values 0.70 upward or downward indicate a strong correlation. From 0.30 to 0.7 positive or negative indicate mild correlation and 0 to 0.30 means poor correlation.

Removing the fruit from the field during the sampling procedure reduces the period when the larvae are susceptible to attack, resulting in underestimated parasitism (Sivinski et al., 1996). Thus, for *D. longicaudata*, the most accurate samples are obtained from fallen fruit in which all larvae matured, but none was left to pupate. Our removal of some maturing beans from coffee plants, not the soil, may have led to substantial underestimates of parasitism rates.

Another explanation for the low parasitism rate in fruit following *D. longicaudata* releases was the naturally occurring low infestation level (puparia/fruit) relative to the host density available in the artificial oviposition devices (Table 2). Female parasitoids may forage longer in locations with a larger number of hosts (Alphen and Bernstein, 2008). Therefore, higher host density in parasitism units might have prolonged host searching. Eighty parasitism units installed in the plantation yielded 3,350 *D. longicaudata* after 24 h and 3,103 after 48 h. In a previous study in a guava orchard, similar units yielded each an average of 36.6 parasitoids after 24 h following augmentative releases (Leal et al., 2008). This was comparable to the average of 41.9 and 38.8 parasitoids per parasitism unit in the present study.

Although parasitism was relatively low, both in fruit samples and in the parasitism units, the parasitoid managed to disperse to larger distances than those recorded in guava orchards. It appears that *D. longicaudata* has a high capacity to disperse in coffee plantations under semiarid conditions. Perhaps the habitat structure of coffee plantations presented fewer physical barriers to the parasitoids dispersal than the guava trees did.

In this study, both the parasitism rate and the average dispersal of the parasitoid recaptured in parasitism units were higher in the first 24 h after release (Table 3). The quick dispersal can increase probability of parasitoids to locate the larvae in infested fruit. However, survival and persistence of the parasitoid in an area depend on a number of factors besides simply the host presence.

The parasitoid dispersal does not seem to be related to climate parameters where it is released (Table 5). Paranhos et al. (2007) correlated the average distance of dispersal (DM) of *D. longicaudata* in citrus orchards, in Piracicaba-SP, Brazil, with climate variables in different seasons of the year. In the summer, climate conditions did not affect the average distance of dispersal and the occupancy area. There was only a small variation of temperature and humidity during the experimental period in the summer. On the other hand, distances reached were greater in the summer than in the winter, probably because of the lower temperature.

The present research showed that both fruit samples and parasitism units might be used to estimate dispersal. The average distances of dispersion and dispersal areas calculated from fruit samples (Table 1) and parasitism units (Table 3) were similar. However, oviposition units are more practical and accurate, since they can be

homogeneously distributed, they hold equal quantities of hosts and are used regardless of the presence of infested fruits in the area.

Our oviposition-based sampling methods did not reflect the numbers of females dispersing a particular distance, only showing that one or more did so. Females may also have passed sample sites without ovipositing, causing dispersal to be underestimated. The use of attractive traps, perhaps baited with either food and oviposition kairomones or both, (Paranhos et al., 2007) might capture *D. longicaudata* engaged in a broader range of behaviors. However, data reflecting the movements of sexually mature females may be the most important in designing effective strategies for augmentative releases.

The elimination of almost 70 % of fruit flies populations resulting from the augmentative releases of about 940 *D. longicaudata* parasitoids per hectare in commercial mango orchards, backyard orchards and native vegetation types was demonstrated by Montoya et al. (2000) in Mexico. The present study leads us to recommend, based on the obtained average dispersal area, that cohorts of 2,000 parasitoids be released in six points per hectare. Furthermore, if augmentative releases are used together with other strategies, such as sterile insect technique and cultural control methods, this can result in significant and important synergistic effects on the suppression of the fruit fly population (Sivinski et al., 1996; Montoya et al., 2000). In the future, additional studies incorporating longer post-release sampling periods could estimate *D. longicaudata* persistence in the field and frequently of releases to keep the desired densities of both the pest and the parasitoid species.

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