Long-Distance Movement of *Bactrocera dorsalis* (Diptera: Tephritidae) in Puna, Hawaii: How far *can* they go?

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Abstract: The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), is considered a major economic threat in many regions worldwide, including the island of Hawaii in the Hawaiian archipelago. The need to control large populations over large areas helped initiate the USDA-ARS (United States Department of Agriculture–Agricultural Research Service) area-wide program. There is some discussion concerning the feasibility of eradication of the oriental fruit fly in areas on the island of Hawaii. An important aspect of population suppression is concerned with the ability of a species to move long distances. Suppression of an area may be futile if source populations outside of that area are capable of moving into and re-establishing populations within the suppression area. While most movement studies focus on the short-distance dispersal of flies from a single release point, this study aimed to explore the longer tails of the dispersal distribution suspected for many tephritids. Four releases of double-marked, sterile, laboratory-reared oriental fruit flies were completed. The releases took place at four different distances from an experimental fruit fly suppression zone within the Puna District on the island of Hawaii. Flies captured in methyl eugenol traps and protein bait traps were collected and examined for the mark. Many flies were recovered at unprecedented long distances (between 2–11.39 km) from the release point. Studies of this nature are notoriously difficult, as replication is not feasible and countless variables complicate procedures. However, we feel extremely fortunate to have collected data confirming results that, to our knowledge, have not been previously observed. These long-distance recaptures aid in understanding the long tails of spatial distribution of fly movement that have been suspected of this species, and will benefit consideration of dimensions for buffer zones that would be needed for the establishment of infestation-free or low-prevalence zones.

Suppose you wanted to know how far an insect could move; not just how far it typically moves, but how far it *can* move. The typical way to study movement is to do a point release and then set traps at varying distances away from this point (often in concentric rings) in order to capture what's known as the "distribution kernel." This is basically an often bell-shaped curve that describes how the insects move away from the release point. The problem is that, as you move away from the trap, your probability of recapture decreases with the square of the distance. It gets harder and harder to trap the insects you want to follow. Capturing what happens in this tail can be quite dicey, but sometimes it's important.

The oriental fruit fly, *Bactrocera dorsalis* (Hendel), native to Southeast Asia (Akertarawong et al. 2007, Koyama et al. 1984), was inadvertently introduced to the island of Hawaii some time prior to its detection in 1946 (Harris 1989). High population levels and the economic impact of this pest species in Hawaii led the USDA-ARS to fund an Areawide Fruit Fly Integrated Pest Management (IPM) Program in 1999 (Peck et al. 2005). The program has focused on population suppression through use of population monitoring, bait sprays, male annihilation, biological control (sterile insect technique (SIT) and parasitoid releases) and field sanitation (Peck et al. 2005, Vargas et al. 2008). Eradication of *B. dorsalis* has been successful in the Mariana and Okinawa Islands in 1965 and 1982 respectively (Steiner et al. 1970, Koyama et al. 1984). Many ecological factors influence the success of lowering population numbers in an area, including the species' ability to move long distances and reinvade areas of suppression. Isolation from other infested areas and assurance there will be no localized failures (Steiner et al. 1970, Plant and Cunningham 1991) are essential to the success of an eradication or even a suppression program. But the question remains, can these fruit flies cross these suppression zone barriers?

Most point-release movement studies of *B. dorsalis* can't address this question. Long-distance movement studies are notably difficult as such movement is often considered to be a rare event (Peck et al. 2005). Stochastic events such as passive transport, extreme weather events, predation, and loss of a mark (with mark-release-recapture studies) can all complicate results. Variables, including length of study, sex and age of flies at release, size of the area sampled for recaptures, capture of strong fliers (Peck et al. 2005) and sterilization by irradiation (Sharp and Chambers 1976, Hamada 1980) can also potentially affect results in misleading ways. Literature concerning the ability of *B. dorsalis* to move long distances is varied and inconsistent. It is generally thought that adult movement is mostly related to host availability (Fletcher 1989), and that tephritids are typically non-dispersive, especially when hosts are plentiful (Fletcher 1987, Peck and McQuate 2004). Vargas et al. (1989) found direct relationships of population buildups between native and cultivated areas on the island of Kauai in Hawaii, suggesting movement corridors between the two areas. While such research has proven useful, information concerning the long-distance movement capabilities has been lacking and will supplement such studies. Simultaneously, a few arguments for long-distance movement do exist in the literature, most of which date to several decades ago. Many of these references appear to be speculative and unsubstantiated. Many refer to a study done by Iwahasi in 1972, in which a few flies moved 50 km over water. However, this study has since proved to be controversial, as it cannot be determined whether the events recorded in the study were due to passive transport by wind. While passive transport is important to control, more information is needed concerning the fly's ability for active transport. Information from a formal mark-release-recapture study in an area with ample host fruit and little chance of passive transport has been lacking in the literature. The main objective of this study was to conduct a formal mark-release-recapture study in order to investigate specifically how far the oriental fruit fly can potentially move.

Because this study is focused on rare events in the movement of this fly, standard statistical assumptions are not met and standard statistical analyses cannot be performed, necessitating a focus on qualitative aspects of movement and the simple recording of movement events. While standard statistical measures cannot be provided in this kind of study, this does not detract from observations describing that the flies did in fact move as far as recorded in this study.

This study was conducted in association with an oriental fruit fly suppression trial in commercial papaya orchards in the Puna District of Hawaii Island, with an aim to see from what distances oriental fruit flies could travel to enter the suppression zone. Such information is needed in order to examine the possibility of establishing infestation-free zones or low-prevalence zones.

Materials and Methods

A 51 km^2 study grid in Puna was established in 2004 with the purpose of implementing and determining the effectiveness of the "1-2-3-4" program (1: population monitoring; 2: sanitation; 3: protein bait; and 4: male annihilation traps) on fruit fly suppression (Mau et al. 2007, Vargas et al. 2008). Each grid was 1.0 km^2 and (depending on roads and accessibility into a grid) contained one trapping station each. One trap was baited with the male lure for oriental fruit fly, methyl eugenol (Scentry Biologicals, Billings, MT), with Vaportape (Hercon Environmental, Emigsville, PA) as a knock-down toxicant. The second trap was baited with Torula yeast pellets (ERA International, Ltd., Freeport, NY 11520), diluted at a rate of 1 pellet per 100 ml, which is attractive to both males and females.

Additionally, trap #32 (Fig. 1) represents a collection of sixteen trapping stations situated closely together. This area was established in earlier years as part of the Hawaii Fruit Fly Area Wide Pest Management Program. About 130 ha at the middle of the study area were planted to papaya; the predominant cultivars were 'Rainbow'

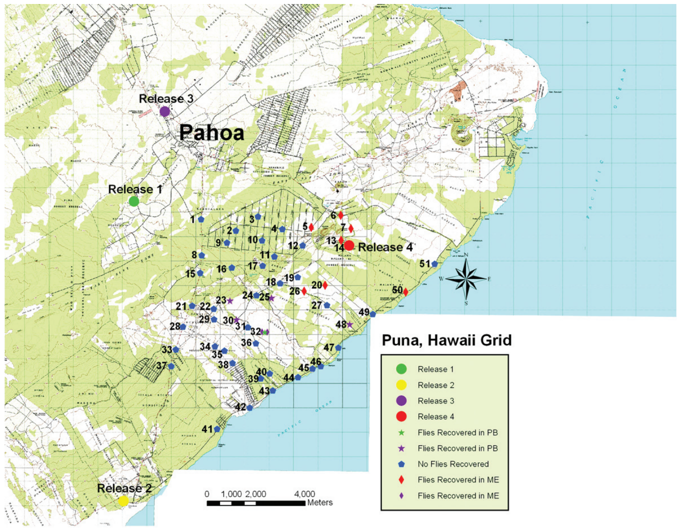

Figure 1. Map of the trapping area with traps in 1 km^2 grids and location of release points.

(≈60%) and 'Sunrise' (≈30%) and the remaining 10% were 'Kapoho Solo' and 'Sunup'. In order to lower the oriental fruit fly population, a total of 540 traps, each baited with 10 g [AI] solid methyl eugenol plugs, were placed throughout these papaya orchards, and extending into the surrounding forest borders (Piñero et al. 2009). Although these traps could not be sampled because of large capture numbers, inaccessibility, and lack of staffing, this played to our advantage for exploring how far the flies could move. The large number of traps and the concentration of papaya plants had the potential to draw the flies to the distances we hoped to capture. Trap #48 represents a collection of 29 protein bait traps in the 130 ha area planted in papaya.

The Puna district area is characterized by agriculture, relatively recent lava flows, and secondary vegetation or native/disturbed forest, which contains many of the preferred host fruits used by *B. dorsalis*, including yellow and red strawberry guava (*Psidium cattleianum* Sabine), common guava (*Psidium guajava* L.), mango

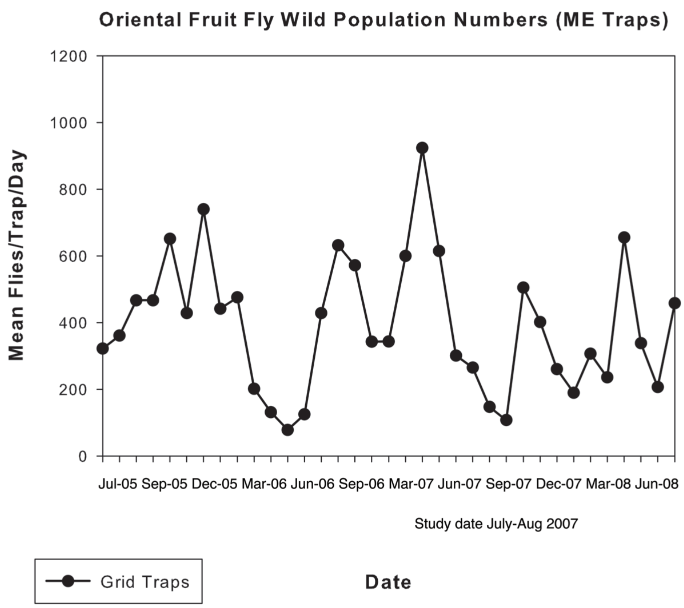

Figure 2. Line graph showing the flies/trap/day trend, July 2005–June 2008. The line graph indicates the fluctuation in wild fly populations through the seasons and years.

Figure 3. The packing station; irradiated pupae were packed in 3.25 oz. portion cups placed in a brown paper bag, which was stapled shut and set inside the 165 oz. paper buckets with screened lids. Agar, sugar, and a protein cake were placed on top of the screened lids and the buckets were relocated to the insectory for the duration of pupation.

(*Mangifera indica* L.), and papaya (*Carica papaya* L.) (Seo et al.1982). With abundant hosts present, the oriental fruit fly has established high population levels in the Puna district (Fig. 2).

The oriental fruit flies used in this study were reared and irradiated (to induce sterility) by the USDA-ARS Pacific Basin Agricultural Research Center in Honolulu, HI. The pupae were coated with Dayglo fluorescent dye (DayGlo Color, Cleveland, OH; Release 1: Neon Red, Release 2: Saturn Yellow, Release 3: Arc Yellow, Release 4: Neon Red) and sent to Hilo, HI. This marker was used in order to differentiate from which release marked recaptures came. In Hilo, 30 mL of pupae were "packed" in 3.25 oz. portion cups (Genpak, Glens Falls, NY) and placed inside brown paper bags, which were stapled and put into screen-covered 165 oz. paper buckets (Sweetheart Paper Buckets, Sweetheart Cup Company, Chicago, IL) (Fig. 3). This was done to facilitate application of the Dayglo dye as the pupae emerged, ensuring encapsulation of dye on the ptilinum and inside the head, and also to simulate a more natural upward emergence. Flies were then kept in an insectory at an average of 24° C with 70% RH. Agar, sugar cubes (99.6% sucrose; C&H Sugar Co., Inc., Crockett CA), and a "protein cake," consisting of three parts sucrose, one part protein yeast hydrolysate (U. S. Biochemical Corp., Cleveland, OH), and 0.5 part torula yeast (Lake States Division, Rhinelander Paper Co., Rhinelander, WI) were placed on top of each screened container. Three random paper buckets were selected each week to determine emergence rates for that week's release. Unemerged, half-emerged, deformed, and dead flies were separated to get an average count of the total "fliers" from the three buckets.

Figure 4. Readmission Ink was applied using a conventional spray bottle after fly movement had been slowed in a cold room.

The flies were marked with readmission ink (Blak-Ray® UVP Inc., Upland California) on the day of release (Fig. 4). This ink, which fluoresces bright yellow under blacklight, was applied for easy identification of recaptured flies. Earlier experiments with the readmission ink proved that the marker was non-toxic and had good retention over five wk (K.M.F., unpublished data). On the mornings of releases 1–3, the paper buckets were placed in a cold room to slow fly movement and all brown paper bags and portion cups were extracted. Flies were placed in a cold room a second time (between 2–4 hours after the first cold room event) until fly movement was again slowed. They were then quickly taken to a spraying station, where the lid was removed and flies were sprayed with ink using an Ace All-Purpose Sprayer (Ace Hardware Corp., Oak Brook, IL). This procedure varied slightly with the fourth release. Cold room time was decreased by extracting the brown paper bags and portion cups immediately before flies were taken to be sprayed with the readmission ink. After spraying the ink, the lid was replaced and the flies were quickly transferred from the bucket into a 1 m^3 holding container.

Figure 5. Immediately following the application of readmission ink, the flies were relocated to a 1 m^3 holding container and transported by van to the release site.

This container allowed sufficient ventilation to dissipate dye fumes while the flies were transported to the release site (Fig. 5).

Release sites were selected according to general distance from the trapping area. Distances from the release sites to the closest trap in the trapping grid were approximately 5 km (release 1), 10 km (release 2), 8 km (release 3), and 2 km (release 4). Because of the prevailing belief that the oriental fruit fly can only disperse short distances, the distances chosen were significantly longer than those deemed necessary to create buffer zones for fruit fly-free areas. A quarantine procedure often adhered to for the Caribbean fruit fly (*Anastrepha suspensa*) is the "Fly-Free Zone Certification Protocol," which requires the designation of 300 acres of land with a 2.4 km host-free buffer zone surrounding the area (Simpson 1993). While the area between a given release and the trapping grid in this study was not devoid of host plants, it was not homogenously saturated

Figure 6. After release from the holding container, flies sought refuge in the shade and cooler temperatures on the underside of breadfruit or noni leaves.

with hosts. Also considered in the selection of release locations was the practicality of receiving permission from landowners.

A shorter distance between the release site and the trapping gird was chosen for the fourth release to increase the probability of recapture and to capture shorter to intermediate distances. Recapturing flies at these longer distances was an untried challenge, and unprecedented in the literature. We could not be sure that we had any recaptures in any of the previous releases and felt we needed to hedge our bets. Due to the close proximity of the fourth release site to trapping locations (0–0.5 km), two traps were removed for the first five days in order to avoid recaptures under 0.5 km. Release 1 occurred on 12 July 2007, release 2 on 19 July 2007, release 3 on 26 July 2007, and release 4 on 2 August 2007 (see Fig. 1 for locations). At each release site, the drawstring on the organza holding container was opened and flies were allowed to leave at will. Dead flies and "walkers" (deformed/non-fliers) were collected and subtracted from our "total fliers" count (obtained by the three random bucket selections mentioned above) in order to estimate a total fly release number. Potential host fruits near the release sites included breadfruit (*Artocarpus altilis* [Parkinson] Fosberg), noni (*Morinda citrifolia* L.), and avocado (*Persea americana* Mill) (Fig. 6). Approximate age of the flies, time of day, and weather conditions were all noted for each release. Four weather stations were located at the following Decimal Degrees coordinates: Puu Kaliu at 19.473546, -154.920268, Kalani Honua at 19.4097, -154.9258, Opihi Rock at 19.5654116350305, -154.895757271562, and AOI at 19.417531, -154.897015.

Figure 7. Flies were collected from both protein bait traps and methyl eugenol traps within the trapping grid on the first and fourth days after each release and collection continued at the same interval until 2 weeks after the last release.

Flies from all methyl eugenol and protein bait traps in the trapping grid were collected on the first and fourth days after each release, and collection continued at the same interval until 2 weeks after the last release (Fig. 7). All trapped flies were put into 1-gallon ZipLoc bags, marked with a date and location, and stored at -80°C until processed for detecting marked recaptures (Fig. 8). Marked flies were easily detected by scanning under blacklight. Four meteorological stations in different areas of the release sites and recapture areas were programmed to record data every 0.5 h for each day of the study. Marked recaptures and spatial dispersion graphs were prepared using SigmaPlot 11.0 (Systat, San Jose, CA).

Figure 8. Due to the high population numbers of the oriental fruit fly in this region, traps often contained hundreds to thousands of specimens. For this reason, a marker was needed that would facilitate quick detection.

Results

Emergence and Release rates

The number of emerged flies varied among the four releases, ranging from 35,530 to 92,781. This was principally due to the inconsistent number of pupae provided weekly from the rearing facility. Single paper buckets were estimated to average between 745 and 935 total "fliers." Over the course of the 4 releases, an estimated total of 217,560 "fliers" were released into the field. Estimated numbers of flies released by week were 43,259 (release 1), 26,507 (release 2), 57,716 (release 3), and, 90,078 (release 4).

Meteorological Data

Weather during the study is summarized in Table 1. In general, most of the rain that we encountered came from tropical storm Cosme. Wind was generally out of the northeast and followed the general patterns of the prevailing trade winds. Wind speed varied among the different averages recorded. Results suggest little variation around the mean, signifying that typical, consistent wind speed patterns prevalent during the long-distance recaptures most likely had little effect on movement. Also, the flight speed of *B. dorsalis*

Table 1. Weather data averaged over course of study

	Min	25th Percentile	Median	75th	Max
Wind Speed mps	0.000	0.360	2.520	3.070	11,500
Wind Direction (degrees from North)	0.00	4.69	8.29	13.7	355.20
Rainfall (mm)	0.00	0.00	0.00	4.71	100.00
Temperature ºC	17.52	21.71	23.24	25.56	31.12

has been recorded at 1.0–1.4 m/s (Sharp and Chambers 1976); only rarely did wind speed exceed this during the study. Mild, constant weather persisted throughout the duration of the study with the exception of tropical storm Cosme, which reached the Puna District one day after the second release (July 19) on July 20 and persisted in the area through July 22. Large amounts of rain fell during this storm. The weather station closest to the release site recorded over 50 mm of rain on July 20.

Recapture and Dispersal of Flies

A total of 1,917 marked (with readmission ink) flies were recovered, giving a recapture rate of 0.009%. Recapture rates also differed dramatically over the four releases. We recorded the following recaptures and rates by release: 1 recapture, 0.0005% (Release 1), 0 recaptures, 0% (Release 2), 23 recaptures, 0.10% (Release 3), 1,887 recaptures, 0.98% (Release 4). For the purpose of this study, any movement over 2 km is considered a "long distance." Thirty flies were captured at distances over 2 km, ranging from 2.63–11.39 km. 73% of these long-distance fliers were recaptured from the third release, 23% from the fourth release, 0.03% from the first release, and zero from the second release. While this study was aimed at long-distance movement, the fourth release has allowed further insight into spatial dispersion. The release occurred at a closer proximity to traps and resulted in 98% of the total recaptures. A total of 1,887 flies were recovered from the fourth release at distances ranging from 0.02–1.90 km. The overall distribution

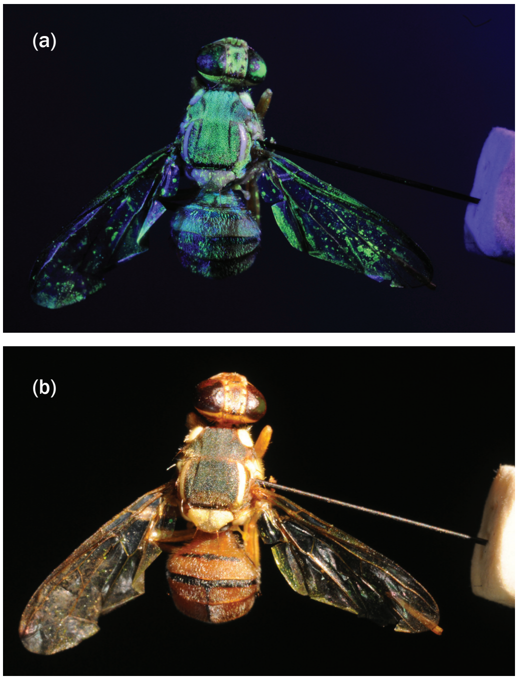

Figure 10. (a) Fly marked with readmission ink under black light and (b) marked fly under natural light.

Table 2: The temporal distribution of marked recaptured flies for all releases. Marked recaptured flies were collected from traps on days 1, 4, 8, 11, and 15 after each release. It is of interest to note the large recaptures of short-distance movement many days after a release, and the abundance of long-distance recaptures only one to four days following a release. Traps less than 0.5 km were set only in Release 4.

	Days Until Recapture			
	1	4	8	>8
0 - 0.1 km release 4 only	No traps set for day one	No traps set for day four	77	218
0.1 - 0.5 km release 4 only	No traps set for day one	No traps set for day four	223	53
0.5 - 2 km	0	2	1,257	51
2 - 5 km	1	1	3	1
5 - 10 km	5	2	0	0
> 10 km	7	9	1	0

with relation to distance can be seen in Fig. 9, which illustrates a distribution with a long and robust tail.

Most (10 of 11) of the flies that were recaptured at long distances were recaptured after a short amount of time (≤ 4 days). Others seemed to persist within an area of 2 km for several weeks. This temporal distribution is given in Table 2. Only in Release 4 were traps set at distances less than 0.5 km, and only after the fourth day for the reasons given above.

Discussion

The experimental design of this study allowed for a succinct depiction of the spatial dispersal of the oriental fruit fly. Several tephritid movement studies have been executed with experimental designs that restrict a fuller understanding of dispersal at longer distances. The results of this study confirm the notion of a leptokurtic distribution with a long tail, indicating the rarer (yet confirmed) long-distance movement capability of a small percentage of the population. Additionally, this was the first mark-recapture field study to use invisible readmission ink (Blak-Ray® UVP Inc., Upland California) as a marker. It was found to be a highly effective marker that met all assumptions associated with a mark-recapture technique (Fig. 10).

It is interesting to note the patterns in the temporal distribution (Fig. 11). While short-distance movement occurred for over 2 weeks, long-distance movement seems to have occurred within a short period of time after a release. Twelve flies were observed to move over 5 km in under one day, and 23 flies moved over 5 km in under four days. Reasons for this are unclear and may be connected to post-teneral activity, as the released flies ranged in age from 2 to 6 days old. Another explanation may be the possibility of overcrowding. As noted in Fig. 2, populations seasonally fluctuate (data collected by USDA-ARS, Hilo, HI). This study was conducted during the months of July and August of 2007, a trough in the mean number of flies/trap/day; therefore, overcrowding may be more realistic during a period of peak population numbers. Plenty of host fruits were found in all four release areas, and according to the consistent wind speed and direction patterns, it is unlikely that flies were carried passively.

Two possible explanations for the absence of recaptures from the second release are the occurrence of the tropical storm Cosme and a low release number of 26,507 (partly due to a low number of

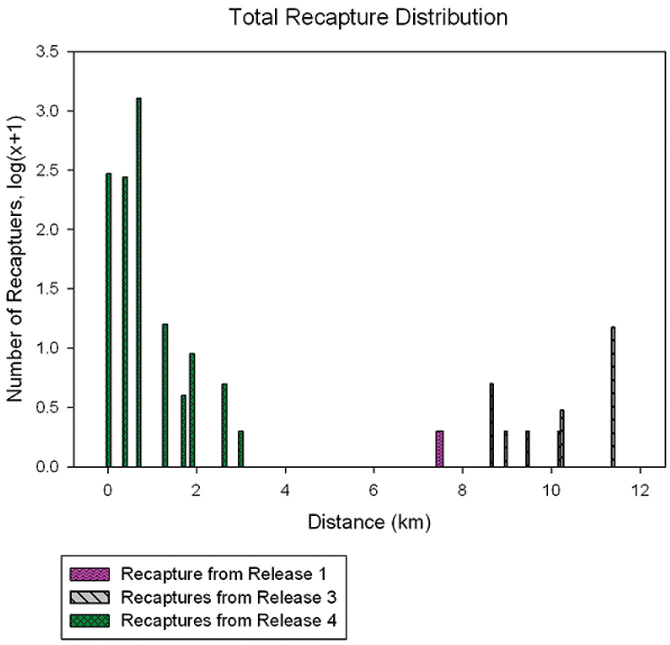

Figure 9. Overall spatial distribution of the total marked recaptures. The initial leptokurtic curve is apparent from short-distance marked recaptures, with a long and robust tail of flies that moved over long distances. Numbers of flies are based on the log(x+1). Each color represents a separate release. The traps in the fourth release were moved closer to the release point to increase the probability of capture.

pupae sent from the rearing lab for this week, resulting in the lowest number of flies released of the 4 releases). Precipitation and wind events during the tropical depression may have increased fatalities and caused the remaining released flies to seek shelter rather than be inclined to movement. This lack of recapture and extreme weather events may be of interest concerning optimal times for SIT after a major storm such as tropical storm Cosme when the population may already be depressed, as SIT works most effectively when population numbers are low.

It is speculated that the differences in release numbers may be due to handling technique (though it must be noted that different amounts of pupae were sent from the rearing lab each week). As explained earlier, on the morning of a release, the flies were prepared for marking. This required cooling the flies in the cold room once in order to clean the fly buckets of emergence cups and bags, and they were cooled a second time in order to slow movement to lift the lid and spray the marker without flies escaping. We speculate that there was some physiological disadvantage with two cold room events in a short amount of time. This, along with the trauma of spraying the marker on the flies, may have increased fatalities. The routine was slightly altered with the fourth fly release. Emergence cups and bags were cleaned from the buckets and flies were then immediately taken to be marked, thus eliminating a second cold room event. This alteration in handling technique seemed to make a difference, as the release number was the highest of all four releases (90,078).

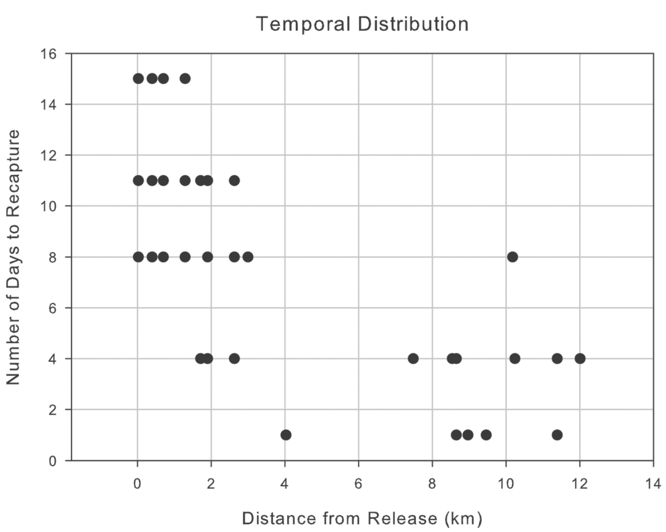

Figure 11. Scatter plot of distance traveled by recaptured flies versus the number of days elapsed before recapture.

The results of this study confirm the ability of the oriental fruit fly to move long distances. Lack of attention to the long tails of dispersion in the past has caused much speculation and misunderstanding concerning the movement ability of the oriental fruit fly. We believe this study to be important quantitative and significant evidence for the long-distance movement capability of this species. These findings should be considered in any control, suppression, or eradication attempts in the future. It is plausible that several individuals moving long distances into a fruit fly-free or low-prevalence zone are likely to aid in re-establishment of a population in that area. For this reason, it would be risky to claim an area is a "fruit fly-free zone" if populations of the species exist even several kilometers outside the suppression area.

Much is still lacking in a full understanding of the spatial dispersion and movement capabilities of the oriental fruit fly (and other tephritids). In this study, distances less than 2 km were so common that they were not considered a long distance. However, even 2 km is a longer distance than some studies in the past have concluded to be a typical dispersion distance. The question remains: when considering movement, how long is "long"?

Mark-recapture studies do not give insight into why the flies move the long distances observed. Several hypotheses suggest that a specific age of the flies or overcrowding can lead to long-distance movement. Mark-recapture studies also do not give insight into whether the movement was one long flight or a series of several small flights or whether the flight was by active or passive transport. All of these issues will require thoughtful studies in the future in order to more fully understand their importance.

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FEATURED INSECT

A *Stauropus* larva in China

Submitted by: Nathan Schiff,
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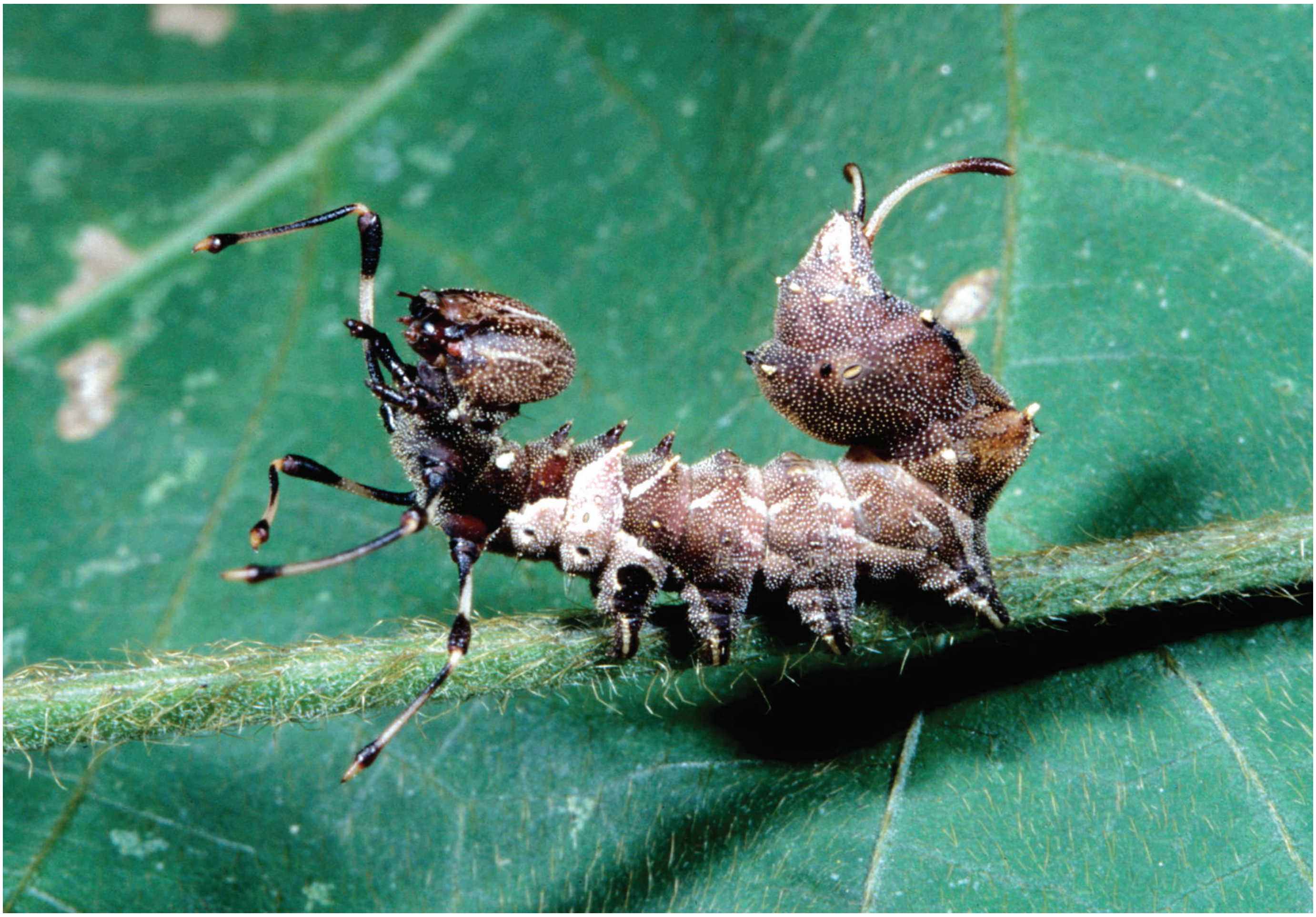

This caterpillar was found while looking for possible biological control agents of kudzu.

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