

## Movement of Sterile Male *Bactrocera cucurbitae* (Diptera: Tephritidae) in a Hawaiian Agroecosystem

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**ABSTRACT** The melon fly, *Bactrocera cucurbitae* Coquillett, invaded the Hawaiian Island chain in 1895. In 1999, a program sponsored by the USDA–ARS to control melon fly and other tephritid pests in Hawaii over a wide area was initiated on the islands of Hawaii, Maui, and Oahu. To control these flies in an areawide setting, understanding how flies move within the landscape is important. To explore the movement of this fly, we examined the movement of marked, male, sterile, laboratory-reared *B. cucurbitae* on the island of Hawaii in an agricultural setting. Two releases of dyed, sterile flies consisting of ≈15,000 flies, were released 6 wk apart. Released flies were trapped back by using Moroccan traps baited with a male attractant. These two releases suggest that in the Hawaiian agricultural areas where the areawide control is being sought, melon flies do not move extensively when there are abundant larval host and adult roosting sites. Over the course of this study, only one fly made it the maximum distance that we could detect fly movement (≈2,000 m in 2 wk). From these data, it seems that the flies dispersed throughout the study area but then moved very little thereafter. This is very apparent in the second release where the recovery rate after the second week was still fairly high, suggesting that if there are plenty of host fields and roosting sites the flies are unlikely to move.

**KEY WORDS** melon fly, wide area control, mark-release-recapture

SOME OF THE MOST DAMAGING fruit pests in the world are found in the family Tephritidae (White and Elson-Harris 1992). For example, these flies severely limit Hawaiian agriculture by causing direct damage to fruits and vegetables and by limiting export markets through quarantines imposed by countries skittish of introducing the pest into their own areas. As a result, Hawaiian fruits and other agricultural products vulnerable to the fly must undergo quarantine treatments before shipment. These treatments are expensive, time-consuming, and lower product quality. If these flies could be effectively controlled or eradicated, it would be a great boon to both individual growers and the agriculture industry in Hawaii.

Four species of tephritid fruit flies have become established in the Hawaiian Islands. The melon fly, *Bactrocera cucurbitae* (Coquillett), invaded the Hawaiian Island chain in 1895, most likely from fruit infested with fly larvae from Japan (Back and Pemberton 1917). It has since become a major pest of cucurbit crops. In 1910, the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), invaded the island of Oahu and by 1918 it had spread to all of the islands in the Hawaiian archipelago (Back and Pemberton 1918). In 1945, the oriental fruit fly, *Bactrocera dorsalis*

(Hendel), was discovered in a shipment of fruit from Hawaii to California. *B. dorsalis* attacks most commercial fruit crops and some native Hawaiian fruits (Harris 1989). The most recent invasion by *Bactrocera latifrons* (Hendel) was detected in 1983 on Oahu (Vargas and Nishida 1985), and it now has spread to all of the main islands where it attacks a number of solanaceous and cucurbitaceous species (Liquido et al. 1994).

**Fruit Fly Movement.** The ecology of these flies is still poorly understood (Carey 1989), and fly movement in particular needs further study, especially in the genus *Bactrocera* (for review, see Fletcher (1989)). There are some studies on related tephritid flies; for example, Plant and Cunningham (1991) studied the movement of *C. capitata*. They found the mean dispersal distance of 248.5 m after 7 d and concluded that most of the flies moved no farther than 1000 m. They further concluded that the fly was not a strong flier and that widespread movement was unlikely. Kovaleski et al. (1999) examined the dispersal ability of *Anastrepha fraterculus* (Wiedemann). They found that most movement was directed to host fruit and that most (90%) of the distribution of flies was contained within 200 m of the release.

Many studies on *Bactrocera* have reported that these flies do not move far (Fletcher 1989). In addition, Aluja (1993) has collected anecdotal information on fly movement that suggested that although most of the population will not move far, some flies have covered impressive distances. For example, marked *B. cucur-*

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*bitae* flies released on Kume Island in the Japanese Archipelago traveled over open ocean 34–56 km among islands, with one male traveling an impressive 200 km (Miyahara and Kawai 1979). S.L.P. (unpublished data) observed a marked *B. dorsalis* traverse an upwind distance of 13 km in a single 24-h period in response to a methyl eugenol-baited trap. Peck and McQuate (2004) have shown that *B. latifrons* does not disperse far from release points in a situation where host plants are numerous.

Movement studies of *B. cucurbitae* have been reviewed in Fletcher (1989). The studies in this review indicate that there are basically two types of movement in this fly: long-distance postteneral movement in which flies disperse broadly after emergence and more localized movement after the discovery of larval host plants. This seems true of both wild flies and laboratory-reared flies (Wong et al. 1986a). Movements within and among local fields dominate after this dispersal period. This study focuses on this latter type of movement.

**USDA–ARS Areawide Fruit Fly Integrated Pest Management (IPM) Program.** In 1999 an Areawide Pest Management (AWPM) program sponsored by the USDA–ARS to control melon fly and other tephritid pests in Hawaii over a wide area was initiated on the islands of Hawaii, Maui, and Oahu (Vargas et al. 2003). The program was designed to lower fly populations over large areas by using a multitiered IPM approach, including pesticide-laced bait sprays (Steiner et al. 1959, Roessler 1989, Deshmukh and Patil 1996), male annihilation (Cunningham and Suda 1995, Hwang et al. 1997), mass sterile male release (Harris et al. 1986b, Wong et al. 1986b, Vargas et al. 1995, Enkerlin and Mumford 1997, Knipling 1998), augmentative parasitoid releases (Purcell et al. 1994, Leonel et al. 1995, Purcell et al. 1998, Vargas et al. 2004), and postharvest field sanitation (Liquido 1993). The program also contained a large educational component designed to help growers, extension agents, and communities better control tephritid flies found in their area.

The first of the tephritid flies that the AWPM targeted was *B. cucurbitae*. This species was chosen for several reasons: 1) *B. cucurbitae* is a major pest of many field crops, including watermelon, squash, tomato, and cucumber; it attacks several wild plants, including bittermelon, *Mormordica charantia* L.; and *Sicyos* sp. (Harris et al. 1986a, Uchida et al. 1990, Iwaizumi et al. 1994); 2) it also has a more limited host range than that found for *B. dorsalis* and *C. capitata* and was thought to be more easily controlled than these two species; 3) it causes significant economic damage and limits planting options of growers in Hawaii as assessed through preprogram surveys; and 4) there are good control measures for this fly including sterile insect technique (SIT), male annihilation, protein bait sprays, and parasitoid release for biological control.

To control these flies in an areawide setting, we must understand how flies move within the landscape. For example, it has been demonstrated that the melon fly does not dwell in fields of larval host plants for

much of the day, provided that the fields are kept relatively weed free. It prefers refuge sites, known in the literature as “roosting” sites, that are protected from the sun, wind, rain, and other weather detrimental (Nishida and Bess 1957, Stark 1995). Common roosting plants include castor bean, *Ricinus communis* L.; Christmas berry, *Schinus terebinthifolius* Raddi; ti, *Cordyline fruticosa* L.; and corn, *Zea mays* L. Some of these preferred roosting sites provide nutrients to the fly in the form of extrafloral nectaries (Nishida 1958), as in castor bean (Wackers et al. 2001), or act as a protein source from pollen, as in corn (McQuate et al. 2003). Thus, the flies are thought to move in and out of the host fields, spending most of their time in the roosting sites (Nishida and Bess 1957, Vargas et al. 1990).

Still, there are many questions about the movement of this fly. Knowing how far the fly can move, how far it is apt to move in different landscapes, and more about its spatial dispersal distribution is important for interpreting trap catch data and assessing whether the fly is being controlled over a large enough area to protect crops from damage. However, there is little information about this aspect of *B. cucurbitae*'s ecology (Vargas et al. 1989, 1990).

To fill in the gap in our knowledge about the movement of this fly, we examined the movement of marked, sterile, laboratory-reared *B. cucurbitae* on the island of Hawaii. Most studies of movement are carried out in regions differing from where suppression attempts will be conducted. This is one of few studies of movement that has been carried out in the same agricultural setting in which suppression is desired. This information will be used to help understand better the ecology of this fly and to provide guidance on the best means to implement targeted control.

## Materials and Methods

**Areawide Activities.** This study was conducted in conjunction with the USDA–ARS's Areawide Fruit Fly IPM Program, which sought to suppress *B. cucurbitae* populations. As part of the suppression efforts supported by this program, a trapping grid covering 40 km<sup>2</sup> was established in the Waimea area of the island of Hawaii. Within each single square kilometer of the grid, a trap was placed, baited with the male pheromone cue lure [CL, 4-(p-hydroxyphenyl)-2-butanone acetate, Cyclo International, El Cajon, CA] and containing one 2.4 by 8.9-cm strip of VaporTape (Hercon Environmental, Emigsville, PA) impregnated with 2,2-dichlorovinyl dimethyl phosphate to serve as a knockdown toxicant.

In addition to the trapping grid traps for this program, traps were added where significant concentrations of larval host plants were found among agricultural and backyard growers' fields (see “Trapping Flies”). The AWPM used four suppression techniques to lower the populations of the fly in this area: bait sprays, sterile insect release, crop sanitation, and biological control. The monitoring traps used in the AWPM also were used for this study. However, these

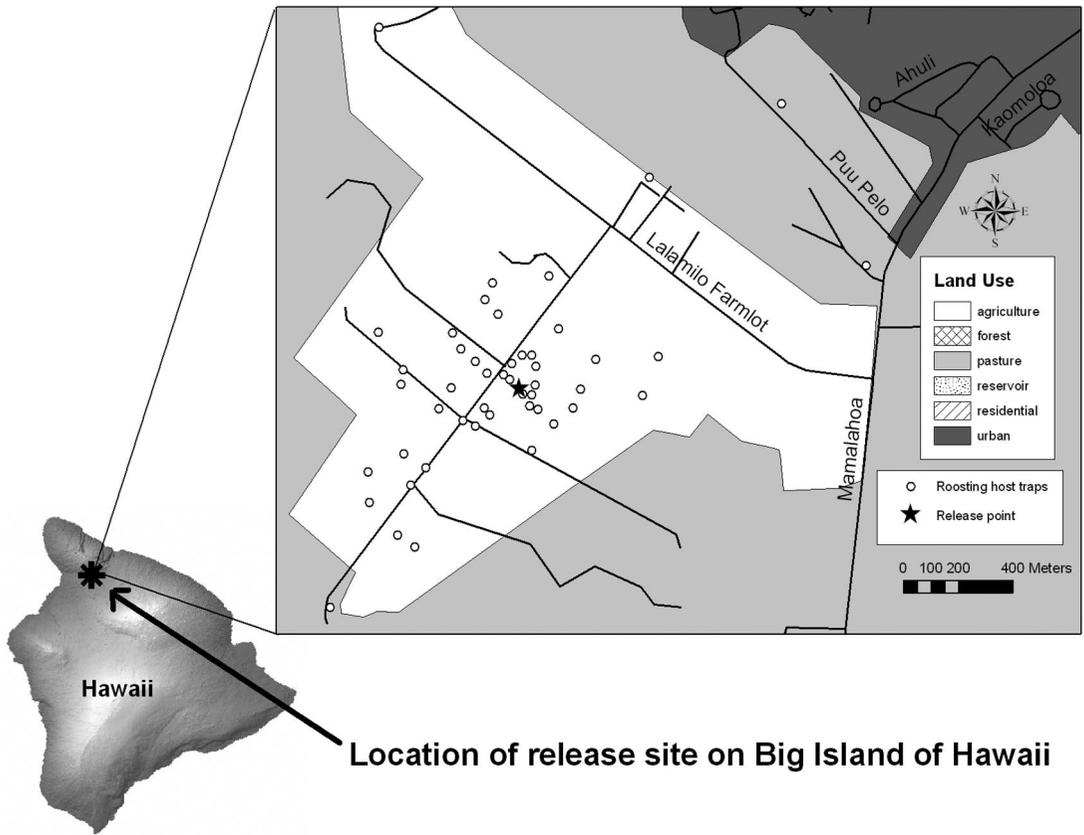


Fig. 1. Location of study on the Big Island of Hawaii.

control activities either had not been started or were suspended during the time the movement study was taking place. More details on the USDA-ARS Areawide program in Hawaii may be found in Vargas et al. 2003.

**Study Site.** The site for the mark–release–recapture was chosen to be within the boundaries of the AWPM in the Waimea region of Hawaii Island, HI, located  $\approx 20^{\circ} 0' 66''$  N and  $155^{\circ} 41' 11''$  W. The part of the grid area for the AWPM is shown in Fig. 1. The release site is found in the Lalamilo area in the southwestern portion of the areawide program area. This is a largely rural agricultural area surrounded by grasslands owned by Parker Ranch. The dominant crops within the release area included corn, melon, and cucumber. Plants considered potential roosting sites also were abundant in the area: corn; sugarcane, *Saccharum officinarum* L.; castor bean; Christmas berry; wild olive, *Olea europaea africana* L.; and milo, *Thespesia populnea* (L.) Sol. ex Corrêa. A weather station recording temperature, humidity, wind speed and direction, and rainfall was set up in the northwestern corner of the release site.

Two releases were made in the center of a 7.9-ha cabbage field surrounded by wild castor bean plants. In the first release, approximately half of the field had been harvested and plowed under and the other half

was still covered with crop plants. The release point was at the margin between the cropped and plowed portion of the field in a place such that the flies could fly over the plowed portion to field margin plants or choose to remain in the cropped portion of the field. In the second release, the field had been completely harvested and plowed.

The choice of this area for this study was made to understand movement of the fly within its actual agricultural context including cropped and uncropped areas. Often, movement studies are made in areas not representative of typical landscape features encountered by wild flies. The emphasis of this study was on movement in a specific landscape setting. As a result, we did not create a regular grid, which would be more convenient to mark–recapture studies, and thus many of the analyses are qualitative.

**Marking Flies.** The flies used for this study were part of a pupal color genetic sexing strain developed by the USDA-ARS Pacific Basin Agricultural Area Research Center in Honolulu, HI (McInnis et al. 2004). *B. cucurbitae* larvae were reared to the pupal stage at the USDA-ARS laboratory in Honolulu. There, the pupae were separated by sex by using a photoelectric sorter and males were irradiated at 100 grays to induce sterility as described in McInnis et al. (2004), who also has shown that release of sterile males is much more

**Table 1.** Host types in which additional traps were set to increase sampling within the release area

Host	Corn	Sugarcane	Castor bean	Christmas berry	Wild olive	Other
No. of traps placed (expected proportion captures if flies were randomly captured with respect to plant type)	2 (0.04)	4 (0.08)	17 (0.35)	12 (0.25)	7 (0.15)	6 (0.13)
Release 1, weighted avg trap catch in first week	0.2265	0	0.5732	0.1348	0.02018	0.04530
Release 2, weighted avg trap catch in second week	0.04401	0	0.3376	0.4195	0.03018	0.1687

Weighted averages are  $[N_h/n_{traps}]/\sum_h N_h/n_{total\ traps}$  where  $N_h$  is the number of flies captured in host type  $h$ ,  $n_{traps}$  is the number of traps set in that host, and  $n_{total\ traps}$  is the total number of traps set.

effective than normal bisexual releases. Male flies were used for this study to avoid grower concerns about female flies possibly stinging the fruit and thereby reducing market value of their crop. The males were sterilized to avoid possible increases that might be caused by the influx of laboratory-reared flies. Before irradiation, the fly pupae were dyed using 5 g/liter fluorescent green dye (Saturn Yellow, Dayglo Color Corporation, Cleveland, OH)

The dyed, irradiated pupae were sent overnight by commercial aircraft to Hilo, HI, and were then transported by motor vehicle to Waimea, HI. Approximately 35 ml of fly pupae was placed in each of 25 wooden cages (19,312 cm<sup>3</sup> each) with one clear Plexiglas side, one rubber side with an access hole covered with a plastic cup, and the other sides screened with mesh screen to allow air flow. [The flies also were treated with a second mark by using a vertebrate protein; for details on method, see Peck and McQuate (2004); however, the assessment of the second mark will be reported in another publication].

To assess the quantity of flies released, number of pupae targeted per holding chamber (1,015 flies) was estimated using a 29 pupae per milliliter volume estimate that has been shown to produce on average the desired number of flies upon emergence. In addition to the targeted number of flies, the quality of flies was assessed. First, the number of flies was counted in one sample bucket packed in the same manner as those used for the releases to see whether the desired number of flies was emerging in the chamber. Next, to assess the quality of the flies released (percentage of fliers), five sets of 100 pupae each were gathered from the pupae that arrived in Hilo and held in separate 9.2-cm-diameter petri plates placed under 8.8-cm-diameter by 20-cm-tall black plastic tubes that had a light film of talcum powder covering the inside surface. The height used for this test of percentage of fliers provides a more stringent test of flight ability than in standard quality control tests where the holding tubes are only half as high (FAO/IAEA 1998).

The flies were provided with water and a food source consisting of three parts sucrose and one part protein yeast hydrolysate (U.S. Biochemical Corporation, Cleveland, OH). The cages were placed in an environmental growth chamber at between 25 and 26°C. The pupae were allowed to emerge as dyed adults within the cages.

The dye is designed such that when the flies emerge from their pupal case, dye particles adhere to much of

the fly's exterior. In addition, upon emergence, the ptilinum of the fly is everted to help open the pupal case. Particles of dye stick to the ptilinum and are permanently incorporated back into the fly's head when the structure is withdrawn into the head capsule.

**Releasing Flies.** In the first release, flies were released on 8 August 2002 at  $\approx$ 9:30 a.m. when the air temperature was 21°C. The cages were carted to the center of the release field. The nearest cover for the flies was  $\approx$ 20 m at the field margin, where the principal roosting host growing along the border was castor bean (*R. communis*). Cages were opened, and flies were allowed to disperse from cages. After  $\approx$ 15 min, the flies remaining in the cages were dumped out, and flies were shooed from the cages by hand. The second release took place 5 wk later on 12 September 2002 at the same place and at the same time. Air temperature was 20°C. The second release of flies was timed such that flies from the first release were no longer being captured in field traps.

**Trapping Flies.** Flies were trapped using Moroccan traps baited with a cotton wick impregnated with 2 ml of CL, an attractant for male *B. curcurbitae*. Traps were hung at a height ranging from 1.25 to 2 m off the ground, depending on the height of the host plant. There were 170 traps distributed within the region that were being used for the AWPM previous to and during this release study. The details of the AWPM trap placement can be found in Vargas et al. 2003, but in short, the AWPM traps were placed in host plants and natural vegetation. In addition, to secure better coverage, 48 traps were placed in various roosting hosts (Table 1) ringing the vicinity of the release point, making a total of 218 traps placed in this area. Figure 1 shows the distribution of these traps relative to the point of release.

**Assessing Recovered Flies for Dye Marker.** All flies recovered were assessed for the presence of the Saturn Yellow dye by examination under a dissecting microscope by using a blacklight to illuminate the fluorescing dye.

**Data Analysis and Experimental Design.** The dispersal distance was quantified by using box plot with quartile confidence intervals. To explore the relationship between the number of flies captured at each location, cubic splines models were individually fit to the number of flies captured at the distance the flies were captured for each week of each of the mark-recapture studies (Fan and Gijbels 1996). Kolmoor-

**Table 2.** Summary statistics for distances of recapture for both releases for each of the five (W1 is first week, and so on.) weeks of study

		Release 1					Release 2						
Week ( <i>n</i> )	Mean (SE)	Min	First Q	Med.	Third Q	Max	Week (N)	Mean (SD)	Min	First Q	Med.	Third Q	Min
W1 (4,671)	75.8 (1.1)	24.6	47.6	50.5	77.3	545.2	W1 (1)	188.3 (.)	188.3	188.3	188.3	188.3	188.3
W2 (112)	267.5 (24.1)	24.6	93.9	230.2	433.2	2136.0	W2 (1379)	135.2 (3.3)	24.6	58.1	60.5	217.6	690.9
W3 (3)	437.9 (4.6)	433.2	433.2	433.2	440.2	447.1	W3 (252)	259.2 (9.4)	24.6	130.7	250	433.2	908.5
W4 (3)	463.2 (15.1)	433.2	453.7	774.2	478.2	482.1	W4 (43)	289.5 (20.5)	50.5	243.7	250	433.2	690.9
W5 (5)	686.9 (121.1)	360.2	433.2	839.4	839.4	962.1	W5 (18)	295.1 (38.7)	124.7	140.6	253.4	433.2	600.8

Statistics include the mean (standard error), minimum (min), first quartile (Q), median (Med.), third quartile, and maximum (max) distance.

gov-Smirnov goodness-of-fit tests (Sokal and Rohlf 1995) were used to compare the empirical distribution function of the flies, by using a stepdown Bonferroni procedure to adjust for multiple comparisons (Hochberg 1988).

Data on wild flies are included to serve as a comparison to the released flies. If patterns are detectible in the wild fly capture distributions, then there may be a problem in the design of the release.

**Results**

During the study, based on readings taken every minute, the wind blew from the north 64% of the time at an average speed of 3.1 (SD = 1.13) m/s and 30% of the time from the north-northwest, the north-northeast, or the northeast at a average speed of 2.2 (SD = 1.10). However, there were no anisotropies noted in the empirical distribution of the released flies.

**Emergence and Flight Ability.** The emergence rate for the flies in the first release was 77.6% and in the second was 83.4%. The number of fliers, as assessed by the flight test, was lower, with 35.4% judged to be fliers in the first release and 39.4% in the second release. Given that we set up ≈1,015 pupae in each cage, we estimate that the number of flies dispersing in the first release was between 8,900 and 20,000 flies. In the second release, the number of dispersing flies was between 9,900 and 21,000 flies. Because the flight test we used was more stringent than normal, we think that the best estimate of the number of flies dispersing is ≈15,000 flies for each release (recognizing the imprecision in this estimate).

**Recapture and Dispersal of Flies.** The recapture rate over the entire study was 19% for the first release and 7% for the second release. Using the approximate numbers estimated from the flight tests, the first release recapture rate was between 53 and 24% and for the second between 16 and 8%. Table 2 shows the dispersal statistics from both releases, which quantifies explicitly the movement of the released flies.

The greatest number of dispersing flies was captured in the first week of the first release in August and in the second week of the second release in September. The spatial distribution of the flies at the end of week 1 in the first release shows a limited dispersal from the release point (Fig. 2a). The wild flies show no relationship to the release point in their spatial distribution (Fig. 2b). Only one marked fly was cap-

tured in the first week of the second release. This delay of peak capture in the second release was likely due to the 5 d of rain events out of seven in the first week of trapping in the second release. In week 2 of the second release, there was a similar dispersal pattern to week 1 of the first release for both sterile flies (Fig. 3a) and wild flies (Fig. 3b).

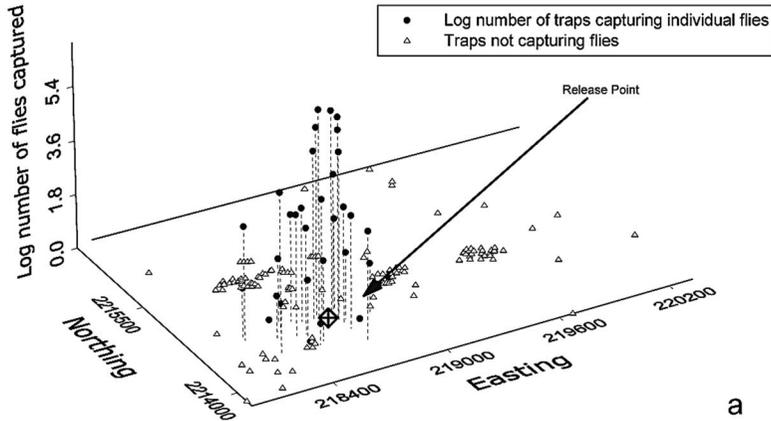
The overall dispersal of the marked flies away from the release point is plotted using box plots (Fig. 4a, first release, and b, second release). Two findings are apparent from these plots. First, the flies did not disperse far from their release point with 95% of the flies not moving beyond 500 m in the first 4 wk of the first release and during all of the second release; however, there is a slow dispersion in median distance traveled away from the release point in the first release that is not apparent in the second release, which seems to flatten out at around 270 m. The maximum distance over both releases traveled by any fly was 2,136 m in the second week of the first release. In the second release, no fly was found farther than 908 m from the release point (release 2, third week). Second, the variance of movement suggests a range of responses from individual flies, from those that move very little to those that move much farther from the release point.

After the first week of the first release and after the second week in the second release, there was a marked drop in the number of flies captured (Fig. 4a, b). After the second week of the first release, there were only 12 more marked flies recaptured, whereas after the third week of the second release (recalling that the second release data seems delayed a week), there were 61 flies captured.

Looking at cubic spline fits shows that the distance relationships between the first and second release are qualitatively similar if the first and second weeks of the first release are compared with the second and third weeks of the second release (Fig. 5a). These comparisons were made because of the apparent lag in the immediate dispersal of the flies in the second release. Figure 5b shows that, as expected, the distribution of wild flies is not related to the release point with correlation between the number of trapped wild flies and distance less than an absolute value of 0.16 for each week and over both releases.

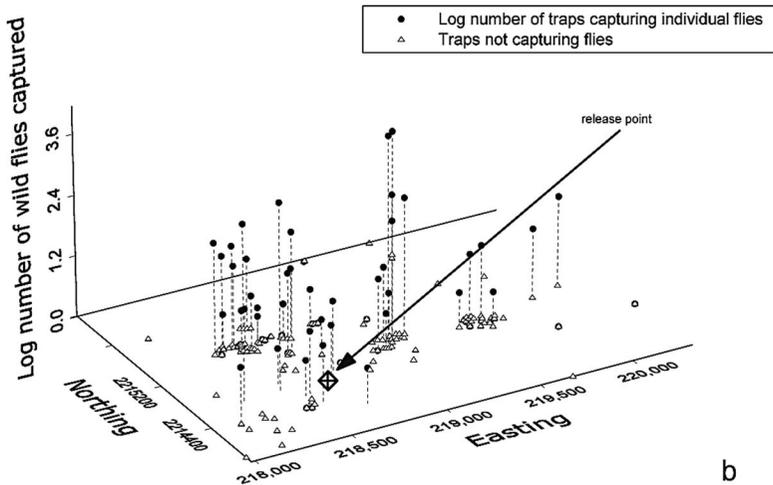
This similarity between week 1 in the first release and week 2 in the second release also can be seen in the plots of the Empirical Distribution Functions

First Release: Week-one trap capture of marked *B. cucurbitae* at given GPS coordinate



a

First Release: Week-one trap capture of wild *B. cucurbitae* at given GPS coordinate



b

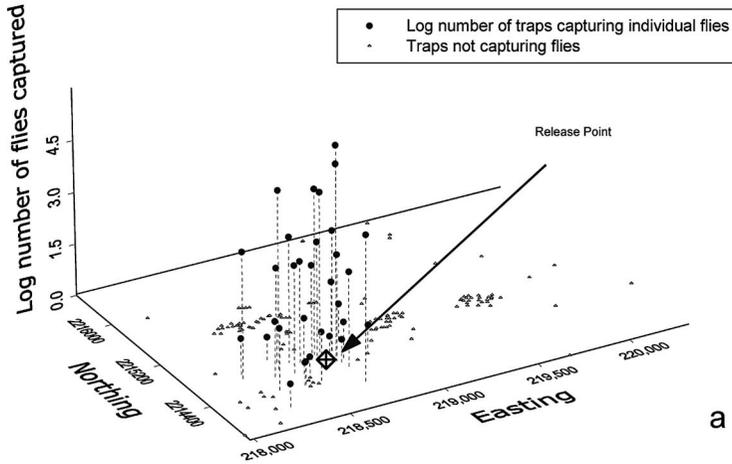
Fig. 2. Location and number of flies caught in each trap in the first week of the first release. The easting and northing dimension give the global positioning system (GPS) coordinates for each trap. The log number of flies captured in each trap is plotted on the vertical dimension. The location of traps not catching any flies is represented by small triangles without a dotted line extension along the vertical axis. The release point is given as indicated. (a) Spatial distribution of laboratory-reared marked and released *B. cucurbitae*. (b) Spatial distribution of wild *B. cucurbitae*.

(EDF) over distance. Although all of the EDFs from the mark-recapture are significantly different from one another by using the Kolmogorov-Smirnov goodness-of-fit test for at least one point ( $P < 0.0001$ ) (Fig. 6a), there is a qualitative similarity between the first and second weeks of the first and second release, respectively, and the second week of the first release and the third week of the second release. As expected in the EDFs of the wild flies (Fig. 6b), none of the distance distributions differed from one another statistically (adjusted  $P > 0.05$ ) using a Kolmogorov-Smirnov goodness-of-fit test and a stepdown Bonferroni procedure to adjust for multiple tests (Hochberg 1988). The EDF plots also suggest that estimation of the daily rate of dispersal over the course of the first

week can be accomplished by comparing the change in the median distance between the first and second weeks in the first release (25 m/d) and the second and third weeks in the second release (27 m/d).

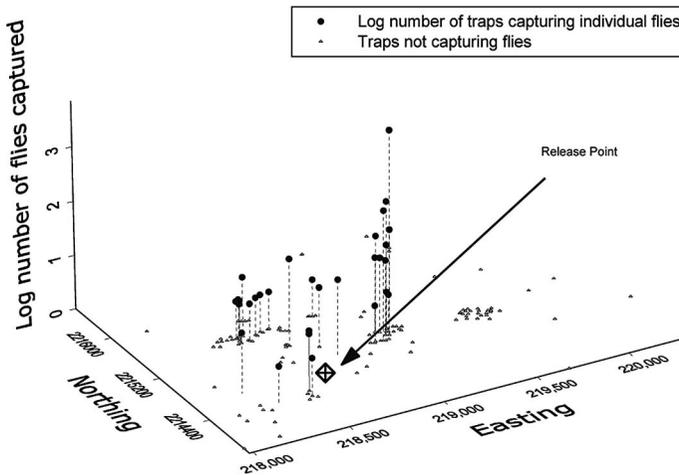
The distribution of trapped flies across the different roosting sites is given in Table 1. It is clear that most of the flies were captured in plants that have been identified as *B. cucurbitae* roosting sites. In the first release, corn was highly attractive with 22% of the flies being caught in corn when only 4% were expected based on the proportion of the traps placed in those plants. Traps placed in castor bean captured 57% of the flies when 35% were expected; traps placed in Christmas berry captured 13% of the flies when 25% were expected. In the second release, however, 42% of the

Second Release: Week-two trap capture of marked *B. cucurbitae* at given GPS coordinate



a

Second Release: Week-two trap capture of wild *B. cucurbitae* at given GPS coordinate



b

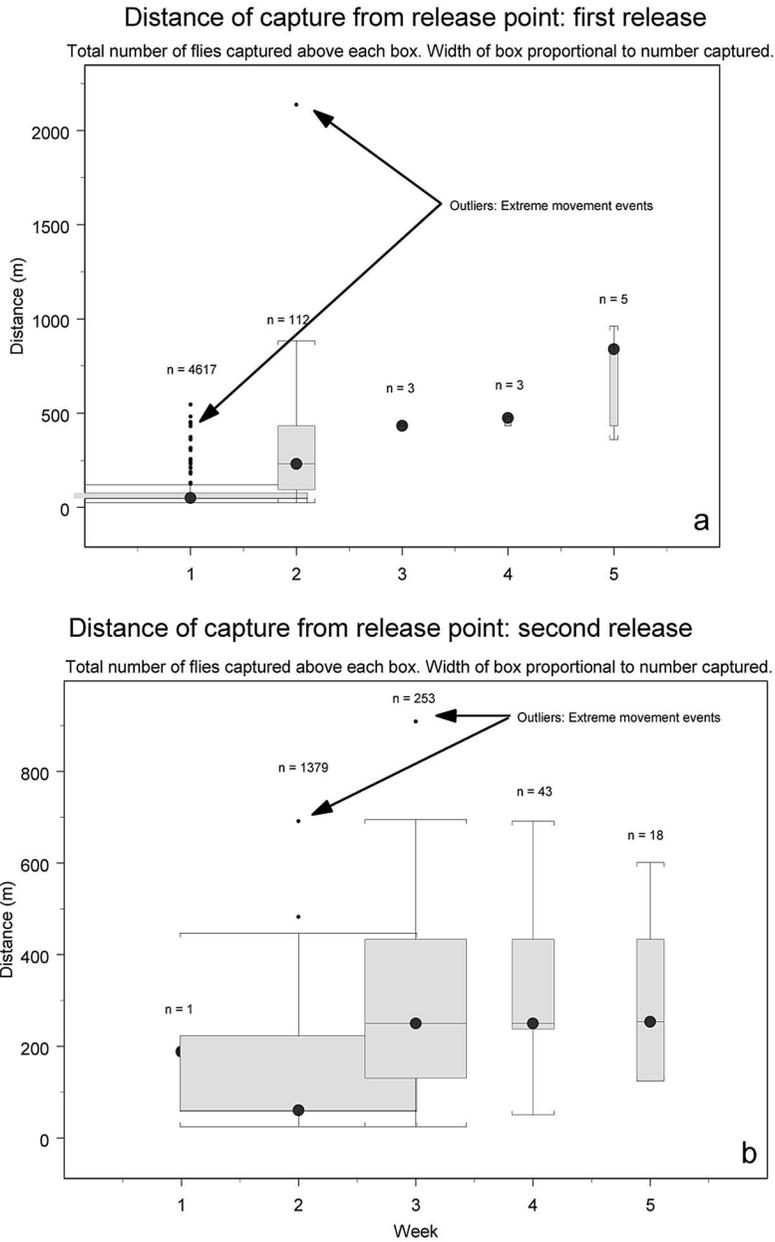
Fig. 3. Location and number of flies caught in each trap in the second week of the second release. The easting and northing dimension give the global positioning system (GPS) coordinates for each trap. The log number of flies captured in each trap is plotted on the vertical dimension. The location of traps not catching any flies is represented by small triangles without a dotted line extension along the vertical axis. The release point is given as indicated. (a) Spatial distribution of laboratory-reared marked and released *B. cucurbitae*. (b) Spatial distribution of wild *B. cucurbitae*.

flies were captured in Christmas berry, 34% were captured in castor bean, and only 4% in corn, suggesting that in the month separating the two releases the attractiveness of Christmas berry increased significantly.

**Discussion**

Aluja (1993) notes that many factors can influence the movement of tephritid fruit flies, including genetics, physiological state, prior experience, sex, body shape as well as biotic and abiotic factors. Several studies have shown that, given the opportunity, these flies can move great distances (Miyahara and Kawai 1979), especially in a postteneral movement event that

has been observed in *B. cucurbitae* (Fletcher 1989). These two releases suggest that in the Hawaiian agricultural areas where the areawide control is being sought, melon flies do not move extensively in an agricultural area with abundant larval host and adult roosting sites. Over the course of this study, only one fly made it the maximum distance that we could detect fly movement ( $\approx 2,000$  m in 2 wk). These data suggest that flies initially dispersed throughout the study area but then moved very little thereafter. This was very apparent in the second release where the recovery rate after the second week was high (Fig. 4), suggesting that if there are plenty of host fields and roosting sites the flies are unlikely to move. Finding what happens in the tails of the movement distribution will

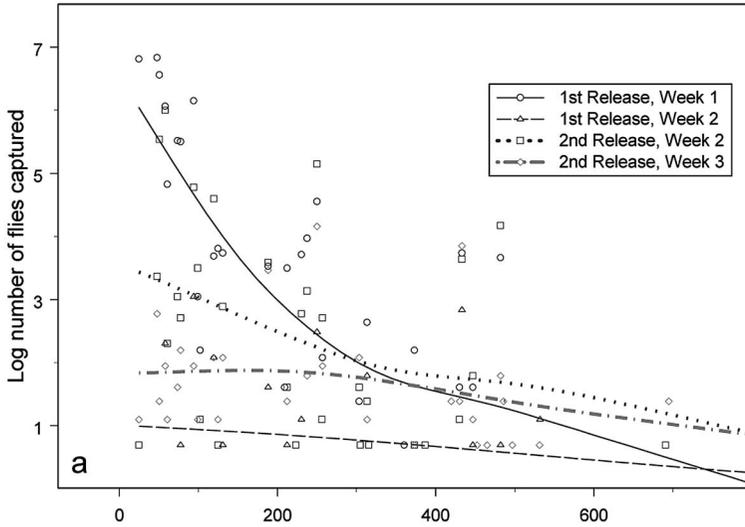


**Fig. 4.** Box plot describing the median and variance in the distance the flies dispersed from the release point. The 25th and 75th quartiles are the top and bottom edge of the box, respectively. The median is represented by the dot and the whiskers represent the fifth and 95th percentiles. The width of the box is proportional to the number of traps containing flies. (a) Box plots of fly dispersal in the first release. There is a precipitous drop in the number of flies captured after the first week, which continues to fall after the second week. There is a slight increase in the median distance traveled through the week. (b) Box plots of fly dispersal in the second release. These flies show no increase in median dispersal after the third week. The recapture rate is lower overall than the first release; however, the drop in the number of flies captured does not drop as steeply.

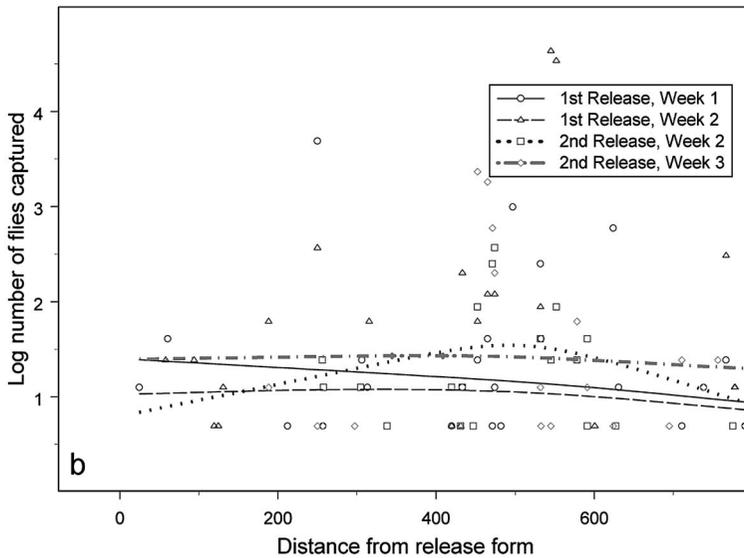
continue to be a problem in these kinds of studies. This is because as the flies move from the release point, the area being trapped increases geometrically, increasing costs and logistic difficulty of more distant trapping, while maintaining a low probability of detecting a fly because these events are apparently rare. A related problem with these types of mark-release-recapture

studies is that it is possible that the most able flies are those captured earlier in the experiment, removing those flies more likely to be the better dispersers. Compounding the problem is the uncertainty of how movement of laboratory-reared, irradiated flies used in this study compares with that of wild fly populations. Hamada (1980) found differences in the dis-

Distance of marked *B. cucurbitae* trap captures from release point



Distance of wild *B. cucurbitae* trap captures from release point

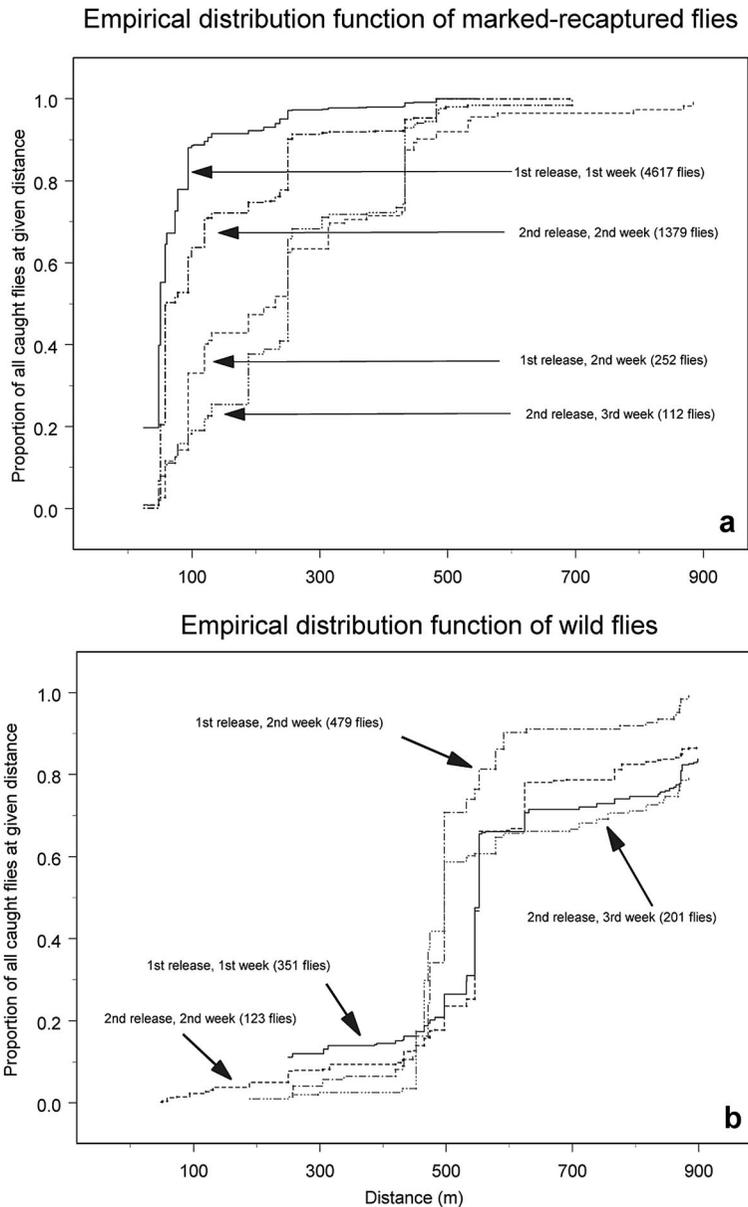


**Fig. 5.** Cubic spline fits of the log number of flies captured versus the distance from the release point they were captured. Weeks 1 and 2 from the first release and two and three from the second release (see text for reasons for the choice of these weeks) are represented. (a) Marked-recaptured flies in the initial week of movement is high and then, in both releases, declines sharply in the second week. (b) As expected, the wild flies show no relationship between the number of wild flies captured and the distance from the release point.

persal ability of irradiated versus nonirradiated flies. This suggests that our estimates of dispersal rates are likely to be underestimates of movement in wild flies.

These types of studies are notoriously difficult (Turchin 1998). There are important questions that must be asked about the meaning of these two releases (Carpenter et al. 1998). Are these releases equivalent to two unreplicated experiments? An experiment replicated twice? The question is not easy to answer and does not fit well in many of the more familiar problems

and questions of experimental design in ecological systems (Hurlbert 1984). At one extreme, one could view each release as a replication in a single experiment in which the agricultural landscape is the treatment and the flies are pseudoreplicates. The idea of treatment here does not really seem to fit. However, suppose we had released 100,000 flies, one could view this as a single experiment replicated 100,000 times in each treatment. Indeed, one could imagine (although it is not recommended) releasing each fly singly and



**Fig. 6.** EDF of the cumulative number of flies found less than the given distance for (a) marked laboratory-reared flies and (b) wild flies for the first 2 wk in the first release and for the second and third weeks for the second release (see text for explanation of why these weeks were chosen for comparison). The total number of flies captured for each plot is noted in parentheses. For the marked-released flies (a) a Kolmogorov–Smirnov goodness-of-fit test indicated that the EDFs were significantly different from one another at least at one point. Despite the significant differences, it is clear that in the laboratory-reared marked flies, the first weeks of trap captures in the two releases are qualitatively more similar than the following week of trap capture, which in turn are qualitatively more similar to each other (a). This is not true in the wild flies (b) where, after adjustment for multiple comparisons, there was no significant difference between EDFs ( $P > 0.04$ ) (after adjustment for six multiple comparisons,  $P$  must be  $< 0.008$  to be significant at the  $\alpha = 0.05$  level). Note: The large jump, particularly prominent in the wild flies, at approximately the 500-m distance is caused by a break in the agricultural landscape of roosting sites so that few traps, and thus few captures were obtained in that region.

measuring its distance from release at various times after release. How does this differ from releasing them all at once? Mark-recapture studies do not seem to fit well into a traditional experimental design framework,

and the special methods designed to explore spatial spread are used here without the expectations of inferential analysis of variance (Milliken 1992). The question begged here is what would happen if we did

more releases? What if we could do 10 or 20 more? This would allow us to refine the movement distribution; but, of course, the resources used to do these two releases were substantial, and it is unlikely that more could have been provided for more releases. However, we suggest that there is information here that will be valuable to those interested in fruit fly movement. Such studies are difficult, and therefore rare, and as such any information is useful and advances our knowledge of fruit fly ecology (Wiens 2001).

Despite these uncertainties, the estimated low-movement rate in the current study has positive implications for area-wide programs designed to control the fly. This study suggests that if agricultural areas are sufficiently isolated, area-wide programs are likely to be successful. However, because of the possibility of rare recolonization events, monitoring will have to be maintained because the flies do seem able to move significant distances if areas are without needed resources such as host plants for oviposition, food, or mates. For example, the effect of crop sanitation may have an effect on the movement proclivity of the fly, with flies more inclined to move if they find insufficient host material. However, there is evidence that this long-distance movement behavior is conditioned on the age of the flies, and several studies have noted that older flies disperse significantly shorter distances than postteneral flies (Nakamori and Soemori 1981, Soemori and Kuba 1983).

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