Inability of *Ceratitis capitata* (Diptera: Tephritidae) to Overwinter in the Judean Hills

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ABSTRACT   The overwintering potential of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), in cold winter areas within its northern distribution is a key element in understanding its ecology. Recent studies have suggested that although originating in tropical Africa, the fly has become adapted to the cold weather that prevails within its northernmost areas of distribution. We address the question of whether the Mediterranean fruit fly has expanded its overwintering range to include the mountains of central Israel. Doing so would imply that the fly has developed either a behavioral or a physiological mechanism to cope with low temperature and/or damp conditions in combination with cold. We monitored adult populations year round, sampling fruit, calculating expected emergence days for overwintering flies, and studying adults captured within dense and sparse apple orchards. We also performed several manipulative experiments to study preimago ability to survive the winter under natural or seminatural conditions. The study was conducted in the central mountains of Israel at 700-m altitude from 1994 to 2003. Comparison experiments also were conducted at 400 m and at sea level. Our results show 1) no adults captured during the winter and spring, 2) an absence of new infestations during the winter and spring, and 3) inability of preimago stages to overwinter in the central mountains of Israel. Thus, we conclude that the fly does not overwinter in the central mountains of Israel. We discuss the ecological and applied significance of our findings.

KEY WORDS   *Ceratitis capitata*, overwintering, cold withstanding, migration

INSECTS, LIKE OTHER ORGANISMS, are forced to deal with environmental variability in both time and space. Climatic variability is the main source of limitation, impeding organisms from further expansion away from their origin. Once an insect species finds itself out of its original habitat, three paths can be taken: 1) local extinction, 2) permanent colonization, or 3) "evolutionary, physiological and behavioral responses," e.g., migration and cold-withstanding mechanisms (Begon et al. 1990). Hence, dormancy and migration are alternative mechanism strategies for dealing with environmental variability (Levin 1992). Although the first path leads to escape in time from an unfavorable environment, the second overcomes the environment by escape in space (Begon et al. 1986). In the temperate zone, climatic conditions are the most important factors for instability in space and time (van Emden and Williams 1974). Therefore, the ability of tropical and subtropical multivoltine, nondiapausing insect species to colonize the temperate zone depends upon their ability to endure the local cold weather by cold-withstanding or behavioral mechanisms. Devel-

oping a behavioral or physiological mechanism is believed to be a lengthy evolutionary process, which may eventually lead to subspeciation or formation of a new species. Hence, one may conclude that most invading pests that successfully colonize new climate regions have been preadapted for it.

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), is a cosmopolitan agricultural pest (Christenson and Foote 1960). Originating in tropical Africa (Kourti et al. 1992), the Mediterranean fruit fly has successfully colonized all continents during the 20th century (Harris 1977). Regions colonized by it vary in host plant range, altitude, and weather conditions (Dowell 1983). Currently the Mediterranean fruit fly's northernmost distribution reaches 41° north in latitude (Fischer-Colbrie and Busch-Petersen 1989).

The Mediterranean fruit fly, like other tropical and subtropical multivoltine, nondiapausing tephritids, is not known to possess either cold tolerance or diapausing ability (Christenson and Foote 1960; Greenberg 1960; Bateman 1972, 1976). Thus, its annual seasonal presence in areas with subfreezing winter temperatures remains unexplained. Laboratory and fieldwork have studied Mediterranean fruit fly low-temperature survival (Carante and Lemaitre 1990). Although lab-

oratory studies have concluded the fly to be highly sensitive to low temperatures (Messenger and Flitters 1954), field studies have claimed that a small percentage of the population manages to survive the winter, even under subfreezing temperatures (Greenberg 1954).

One of the most significant studies concerning the Mediterranean fruit fly overwintering mechanism in cold regions took place in northern Greece, close to the northernmost boundary of its distribution limit. Papadopoulos et al. (1996, 1998, 2002) suggested that the Mediterranean fruit fly overwinters mainly in late apple varieties, and they predicted that adults would emerge from March to May accompanied by a simultaneous infestation of early hosts. To support this hypothesis, they set up a high-density trapping grid (1994–1995) and tried to capture overwintering flies and detect early summer infestations. Yet, the first adults (males) captured and first infested hosts detected by them were only from mid-June 1994 and early July 1995 and at the end of June 1998 (Papadopoulos et al. 2000). The first infested host was detected on September 1998 (Papadopoulos et al. 2001). Although these findings did not support their "local overwintering" hypothesis, they retained it, assuming they had failed to detect the spring population and early infestations due to "limited fruit sampling" (Papadopoulos et al. 2001).

In the present article, we address the question of whether there is evidence for overwintering of *C. capitata* in the central mountains of Israel. We have studied this dilemma by conducting several experiments, each designed to examine a particular prediction. In some cases, we used several experiments to study a single prediction. Our null hypothesis, suggested by Israely et al. (1997), is that the Mediterranean fruit fly overwinters locally in the central mountains of Israel. This suggestion was based on finding flies early in the summer and late in the fall in a particular late apple variety orchard. Together with the notion that the fly population is local in this region, this information led them to assume that the flies overwinter as larvae protected inside late apple varieties, even though no flies were detected during the winter and spring. In this article, three predictions are put to test to study the hypothesis that the Mediterranean fruit fly survives locally in the central mountains of Israel through one or more of its life stages, i.e., adult, larvae in fruit, or pupae in soil: 1) overwintering flies should be captured during early spring, and infested hosts should be simultaneously detected; 2) areas with more apple orchards (proposed as a main overwintering host; Papadopoulos et al. 1996) should present higher population in early summer; and 3) preimago *C. capitata* should survive the winter. In addition, we calculated the theoretical latest expected emergence date for overwintering flies and compared it with actual monitoring data. Finally, we studied the adult's ability to survive and infest spring hosts under natural conditions.

Materials and Methods

Experimental Period, Site, Hosts, and Climate. The study was conducted from 1996 to mid-2003 at three sites, which are located in the center of Israel. The main site is located in the Judean Hills and comprised an area of $\approx$10 km^2, surrounding Kibbutz Zova (31.5° N latitude, 700 m above sea level, "high altitude") (Fig. 1). The area is characterized by typical Mediterranean nonhost trees such as pistachio, *Pistacia vera* L., and oak, *Quercus* spp. Wild fig, *Ficus carica* L., is the main host for the Mediterranean fruit fly in this region. Other hosts include commercial deciduous fruit orchards and various ornamentals in the residential zone. The climate is Mediterranean; a warm dry summer and a wet winter with temperature rarely falling below 0°C (for additional climatic data, see Israely et al. 1997). The second and third sites were used during winter 2002 and 2003 for overwintering experiments. One site was a home garden (50 by 50 m) in Mesilat-Zion, 400 m above sea level ("medium altitude"), 10 km west of the main location in Zova. The climate there is characterized by a milder winter, with rare occasions of temperature falling below 0°C. The third site was a home garden (10 by 10 m) in the city of Ashdod at sea level ("low altitude"), on the Mediterranean Sea coast, characterized by a very mild winter temperature (Fig. 2).

Adult Monitoring and Fruit Sampling. Adults were monitored in Zova from 1994 to 2003 by using the method applied by Israely et al. (1997) for year-round adult monitoring, i.e., using a modification of a Steiner trap (White and Harris 1992), baited with the male attractant Trimedlure with the toxicant Dichlorvos (Makteshim Ltd., Be'er-Sheva, Israel). This monitoring method has been successfully used for many years as a basis for Mediterranean fruit fly control in Israel. Two milliliters of Trimedlure was added in every trap and refilled as necessary. Traps were serviced at least once a week, and fly numbers were recorded. During 2000–2003, in cases when numbers were large (>50), fly quantity was assessed by volume by using a standard 50-ml tube. The number of flies was calculated using a linear relation ($n = 97$, $R^2 = 0.98$, $P < 0.001$). The number of traps varied through the years from 1994 to 2001, respectively, as follows: 70, 132, 133, 123, 165, 147, 20, and 20. During 2002, a single trap was suspended in each of the home gardens in the "preimago winter endurance" experiment (three in total). In 2003, additional McPhail dry traps baited with commercial formulations of female-targeted food-based attractants (Biolure, Consep, Bend, OR) (Katsoyannos et al. 1999) were suspended in home gardens 10–20 m away from Steiner traps at 100-, 400-, 600-, and 700-m altitude.

Winter and spring hosts in Zova's residential area include citrus spp. (27 trees), loquat, *Eriobotrya japonica* (22 trees); apricot, *Prunus armeniaca* L. (28 trees); cherry, sweet and sour (17 trees); and commercial sweet cherry orchards, *Prunus avium* L. (700 trees). Fruit was sampled weekly year round from 1994 to 2001, and monthly from December to Sep-
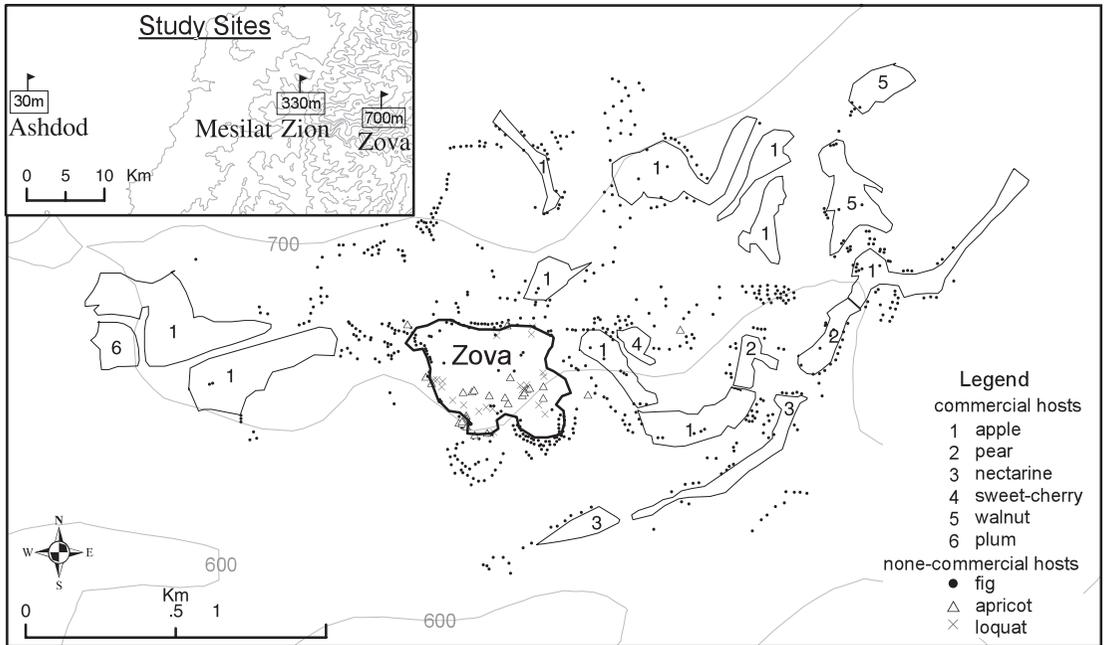
Fig. 1. Main study area surrounding the residential area of Kibbutz Zova, and principal hosts. The inset map presents the relative locations of the three study sites.

tember 2003. Hosts were inspected for infestation under a magnifying glass or a binocular microscope and dissected whenever necessary. The following number of fruits were examined weekly, commencing two months before fruit maturation from January to June: citrus 100–500; loquat 200–500; apricot 300–700 and cherry 500-2000.

Fly Release–Recapture. To study the ability of flies to endure springtime weather conditions at high altitude and to infest early-season hosts, laboratory-grown flies were marked, released, and recaptured. Because rate of dispersion was not the issue of study, we did not place traps >3 km away from the release points. The early hosts (citrus, loquat, and cherry) were inspected for infestations by the flies. Releases took place on 3, 15, and 28 April 1999. Temperatures

during this period ranged from 6.6°C to 36.7°C, with a total precipitation of 37.9 mm; all the precipitation occurred during the week after the first release. The laboratory-released flies were of wild origin ('Zan Sade' type) and were constantly mixed with wild flies to preserve their typical genetic composition. Every 3 yr, cultured females were mated with wild-origin male flies, and the process was repeated with their progenies for three more generations. Flies used in this experiment were the progenies of a culture last introduced to wild males on March 1999. In each experiment 50,000 pupae, with an approximate sex ratio of 1:1, were taken from the laboratory 1 d before emergence. The pupae were first mixed and dyed with fluorescent color (Day Glow, Radiant Color, Houthalen, Belgium) at the rate of 2.8 g/kg pupae, and then
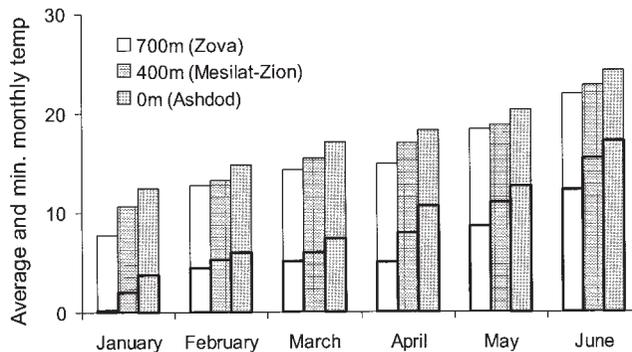

Fig. 2. Average monthly temperatures in Centigrade (bars) and minimum monthly temperatures (boldface lines) from January to June 2002 at the three study sites.
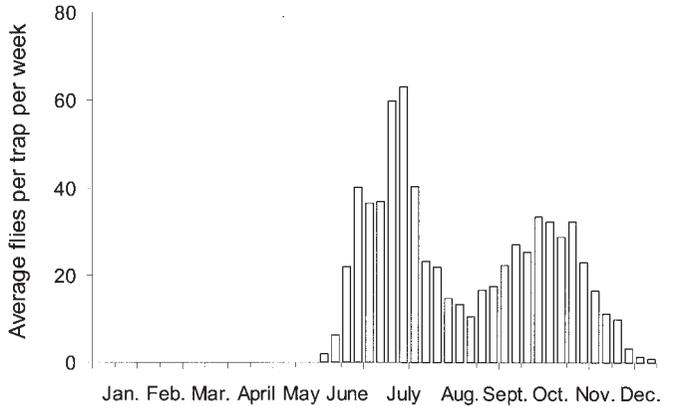
Fig. 3. Average perennial (1994–2001) weekly fly catches in the Zova area (700 m).

packed and kept in paper bags until release. After 1 d, the bags were opened and flies were released early in the morning (0700 hours). Bags containing pupae that had not yet emerged were left in the field until emergence was completed. The first two releases took place in the center of Zova's residential area and the third 1.5 km to the west. The released flies were monitored every 1–2 d, and as catches decreased monitoring shifted to 4–7-d intervals. A grid of 147 Steiner traps baited with Trimedlure was deployed throughout the experimental site. Each of the flies captured during the period of the experiment was examined under a UV light to distinguish between laboratory and wild-origin flies. The same technique made it possible to distinguish between different releases, because flies were dyed with a different color in each release.

Preimago Winter Endurance. Emergence success of preimago from 1) laboratory pupae; 2) naturally infested fruits; and 3) soil under apple trees was studied in Zova, Mesilat-Zion, and Ashdod under natural and seminatural (i.e., protected from rain) conditions.

Laboratory Pupae. Two hundred 1-day-old pupae were placed in plastic boxes (30 by 20 by 15 cm) on

11 January 2001 in Zova and 16 January 2002 in Mesilat-Zion. Pupae, obtained from laboratory-cultured 'Zan Sade', were placed on a 5-cm layer of local soil and then covered by an additional 2 cm of soil. The bottoms and tops of the boxes were made of insect-proof screen, so that rain could enter and exit but insects could not. To prevent the insects from damaging the lower screen, as experienced in the past, the boxes were placed in the field under a tree canopy, on a shelf 1 m above ground. We inspected the boxes daily until July and recorded emerging flies. After ensuring that no flies remained in the boxes, they were disposed of in August. Control boxes were kept indoors at room temperature (24–25°C).

Emergence from Naturally Infested Fruits. Two experiments were performed. 1) During November–December 2000, infested apples (recognized by a typical puncture of the Mediterranean fruit fly ovipositor) of late cultivars ('Golden Delicious' [lsq b]GD] and 'Granny Smith' [GS]) were collected from a commercial plot in the study area. Depending on their size, 6 to 13 apples of one cultivar were then placed in each of 3 to 18 boxes on a local soil (Terra-

Host Type	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Citrus spp.												
Loquat												
Sweet Cherry												
Sour Cherry												
Apricot												
Early Apples var.[1]												
Plum												
Pear												
Nectarine												
Mid Apple var.[2]												
Grape												
Fig												
Late Apple var.[3]												

1 - e.g. Muli-Delicious, Gala; 2 - Golden Delicious; 3 - Granny Smith

Fig. 4. Periods of ripening and sensitivity to Mediterranean fruit fly attack for hosts in the Zova study area (1994–2001). Gray cell denotes detection of infestation in host; striped cell denotes uninfested host; and blank cell indicates lack of fruits susceptible to oviposition.
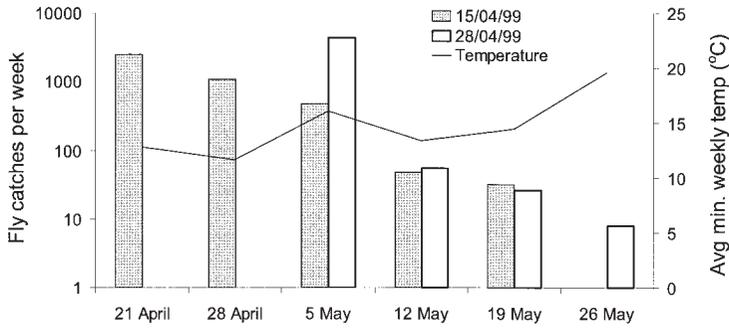
Fig. 5. Total male flies recaptured per week from releases on 15 and 28 April 1999, together with corresponding average minimum weekly temperature. On each date, 50,000 flies (male and female) were released.

Rosa) and then placed on shelves 1 m above ground and inspected daily until August 2001. In addition, five boxes containing GS apples were placed outside under a roof, protected from the rain. 2) On 22 November 2002, infested GD apples were collected from a commercial orchard in Rosh-Tsurim (800-m altitude) and placed in boxes in Zova and Mesilat-Zion, at altitudes of 700 and 400 m, respectively. Sixteen boxes were used at each altitude, with eight placed over a bedding of 4 cm of sandy soil and another eight over Terra-Rosa soil. For each soil type, four boxes were located under a roof to achieve protection from rain, and the remaining four were left unprotected. Boxes were visited daily until mid-May 2003, and emerging flies were counted and removed.

Emergence from Soil under Apple Trees. From March to June 1997, 10 plastic tent-shaped traps were placed on the ground in a late-variety apple orchard in Zova. Each trap was constructed of a thick black nylon sheet, which was placed on the ground. The center of the sheet was elevated 1 m above ground and punctured with a 10-cm hole in which a transparent bottomless trap was placed. The inside of the transparent trap was covered with insect glue ('Frutect', Pal Ltd., Israel) to capture insects drawn to the light. Five nylon tent-shaped traps (each 4 by 5m) were placed between a row of Golden Delicious and a row of Granny Smith trees. An additional five replicates (each 2 by 4 m) were placed between trees within a Golden Delicious row. Most of the area was shaded, so we expected temperature elevation due to the black nylon to be minimal. A control nylon tent-shaped trap was placed for a single week in June 2001 under an apricot tree in Zova.

Calculation of Expected Emergence of Overwintering Adults. Calculation of the expected emergence date for eggs laid on 15 November and 15 December 1998–2002 was done by computing specific stage degree-days (DD) from egg to adult, in total 324.4 DD (Bodenheimer 1951). We used hourly temperature data obtained from a local meteorological station to calculate degree-days for each day. The following equation was used to calculate DD for each stage (Fletcher 1989): $K = y (x - t)$, where K is the thermal constant in degree-days units, y is the time at a given temperature in days units, x is the average temperature

in Centigrade, and t is the lower developmental threshold. To test the validity of the parameters used for calculations, we applied the formula to data obtained from laboratory flies grown under a constant temperature of 25°C (R. Akiva, personal communication) and compared the expected emergence time with the actual trapping data from the study area. To ensure homogeneity of the actual trapping source, a single trap located in a very large home-garden was chosen. We found this trap to be representative of the beginning and ending of trapping in the study area.

Apple Orchards as an Overwintering Refuge. To study the hypothesis that apple orchards are used as an overwintering refuge, we chose two distinct mountainous regions, one with very few apple orchards and the other with extensive areas of apple orchards: 1) The Judean Hills (700–900 m above sea level) are in general a nonagricultural area containing ≈50 ha of apple orchards. Within this region, three settlements were chosen: Zova, Ma'ale-Ha'Hamisha and Ein-Nakoba. Zova is surrounded by 21 ha of apple orchards, whereas Ma'ale-Ha'Hamisha and Ein-Nakoba do not grow apples at all and are surrounded by little agriculture of any kind. 2) The Upper Galilee and the Golan Heights (700–900 m) are the main apple-growing areas of Israel, with 600 and 1,600 ha of orchards, respectively. Two apple-growing settlements were chosen in the Upper Galilee (Yiftah and Manara), having ≈128 ha of orchards, and two in the Golan Heights (Ein-Zivan and El-Rom), with ≈225 ha. During 1996–2001, 65, 64, 68, 67, 68, and 67 traps, respectively, were deployed in the northern mountains (≈15 in each of the four settlements); and 133, 123, 165, 147, 20, and 20, respectively, in the Judean Hills. We compared the average monthly trappings from June to September (1996–2001) for the two regions, expecting that the overwintering population (i.e., the population in spring) would be higher in the region of dense apple orchards than in the lower density region.

Statistical Analysis. The effects of altitude (a surrogate for temperature), exposure to precipitation and soil type on *C. capitata* emergence success from Golden Delicious apples were analyzed using analysis of variance (ANOVA) (Sall et al. 2001; JMP Start Statistics).

Table 1. Adult emergence success from infested apples as a function of altitude (2000–2002)

Origin	Date of collection/pupation	Altitude	Variety	No. fruits	No. boxes	No. flies to emerge
Natural infestation	6/11/2000	700	GD[a]	64	6	0
	23/11/2000	700	GS[b]	125	18	0
	3/12/2000	700	GS	103	10	0
	3/12/2000[c]	700	GS	68	5	0
	6/11/2000	Control[d]	GD	42	4	424
	23/11/2000	Control	GS	22	3	4
	3/12/2000	Control	GS	22	3	1
Laboratory pupae	11/1/2001	700		200 pupae	1	0 (0%)
	16/1/2002[c]	400		200 pupae	1	76 (38%)
	11/1/2001	Control		200 pupae	1	152 (76%)
	16/1/2002	Control		100 pupae	1	68 (68%)

[a] Kept under a roof.
[b] 25–26°C.
[c] Adults ceased to emerge when rain began.

Results

Adult Monitoring. From 1994 to 2003, no flies were trapped during the winter and spring in the main study area, located in the central mountains of Israel. The first flies were trapped from late May to early June. Continuous catches occurred through the summer and fall, peaking in July and again in October, and ceasing at the end of December (Fig. 3). During the spring and early summer of 2003, adult monitoring at the low altitude (100 m) captured flies by both the Trimedlure- and Biolure-baited traps almost weekly, except for several weeks in February–March when there were no catches using either trapping system. At 400, 600, and 700-m altitude, the Trimedlure-baited traps caught flies on 11 May, 16 June, and 31 May, whereas the Biolure-baited traps caught flies on 20 May, 16 June, and 22 May, respectively. Thus, both trapping systems provided essentially the same indication of the existence of adults.

Host Infestation. From 1994 through 2003, no new infestations were detected during the winter and spring (January–May) in winter (citrus species) and spring hosts (sweet cheery and loquat). The only exception was spring 1999, when laboratory flies were deliberately released as described below. The first infested fruits were detected in June, but not before traps had detected flies. Apricot and sweet cherry were the first to ripen after the loquat and the first to be infested. The extent of damage varied between 40 and 70% in the untreated sweet cherry (in home gardens), and between 50 to 100% in apricot. It should be noted that the sweet cherry culture in the study area included a commercial plot containing nine different varieties ripening from early May to late June. None of these were damaged before June (Fig. 4), in spite of the complete absence of insecticide treatments until June.

Fly Release–Recapture. Flies released on 3 April 1999 were confronted with harsh weather conditions such as heavy rain and low temperatures, and thus most died within a short time after release. From ≈25,000 males released only 43 were recaptured during the following 11 d, and none was detected thereafter. Flies from the second release (15 April) and the third release (28 April) were recaptured as late as a month after their release (Fig. 5). As a result of the second and third releases, infested loquats were detected at the end of April on home garden trees. This is the first recorded incidence in which infested loquats were found in the study area. No infestation took place in other years when no flies were released. In 1999, the first wild flies were monitored only on 21 May.

Preimago Winter Endurance. *Laboratory Pupae in Soil.* No adults emerged from pupae placed in the ground and exposed to outdoor conditions at 700-m altitude during 2001. At 400-m altitude, flies started to emerge 53 d after having been placed in the soil (on 16 January 2002). A week later, as rain began, fly emergence ceased (16 March 2002). A total of 76 flies (38% of total pupae) emerged during this period. The control pupae kept at room temperature had 68 to 76% emergence successes (Table 1).

Emergence from Naturally Infested Fruits. Whether protected or unprotected from rain, and regardless of the type of soil on which the apples were placed, no adults emerged from infested apples at 700-m altitude during the 2000–2001 or the 2002–2003 experiments (Tables 2 and 3). At 400 m, the average number of flies when protected from the rain was an order of magnitude higher than when not protected, for both soil types. To further examine the effect of soil type and protection from the rain at 400 m, we performed a two-way ANOVA on the data summarized in the lower half of Table 2. We found that the effect of protection from the rain was highly significant ($F = 39.2$, $P < 0.0001$), but there was no significant effect of soil type ($F = 1.4$, $P = 0.266$). The effect of protection was not significantly different for the two soil types (i.e., there was no interaction; $F = 2.34$, $P = 0.151$).

Emergence from Soil under Apple Trees. No flies were caught emerging in the spring from soil in the apple orchard, neither between rows nor within them. The control plastic tent-shaped trap placed in the summer under an apricot tree caught several flies, confirming the effectiveness of the trapping technique.

Table 2. Emergence per fruit from naturally infested Golden Delicious apples collected on 22 November 2002

Altitude (m)	Accessibility to precipitation	Flies per fruit			
		Sandy soil		Terra Rosa	
		Mean ± SD	No. fruits	Mean ± SD	No. fruits
700	Protected	0 ± 0	41	0 ± 0	43
	Unprotected	0 ± 0	40	0 ± 0	40
400	Protected	4.52 ± 0.67	44	3.07 ± 0.78	44
	Unprotected	0.35 ± 0.22	41	0.55 ± 0.2	41

Comparison of Expected and Actual Emergence Times of Overwintering Adults. Expected emergence time of adults from eggs laid on 15 December was calculated as 24 April 1999, 22 April 2000, 31 March 2001, and 13 April 2002. However, in those years the first wild fly was actually monitored 4, 5, 7, and 7 wk, respectively, later than predicted (Fig. 6). When the more realistic starting date of 15 November was used in the degree-days calculation, the gaps between expected emergence time and date of actual trapping increased to 8–12 wk. For the control flies, the observed developmental period was as predicted from the formula (i.e., 27 d in 25°C from egg to adult).

Apple Orchards as an Overwintering Refuge. In the mountains of Israel, fly trapping began early in June and lasted until December. Average fly trapping during June through September was 2 orders of magnitude higher in the Judean Hills located in the central mountains, having low orchard density, than in the high orchard-density region of the northern mountains. In the latter, the Golan Heights showed a consistently lower average trapping at the onset of summer than the Upper Galilee, in spite of its larger apple-growing area (Fig. 7).

Discussion

Like other tropical-origin fruit flies, the Mediterranean fruit fly does not possess a cold-withstanding mechanism (Christenson and Foote 1960, Greenberg 1960, Bateman 1972, Carey 1984), yet it thrives in the summer in regions where subzero temperatures occur in the winter. For ecological and practical reasons, it is important to determine the mechanism maintaining the Mediterranean fruit fly in such areas. Three alternatives have been suggested to explain the successive appearance of a summer population in the cold areas: overwintering through adults (Messenger and Flitters 1954, Bateman 1972, Carante and Lemaitre 1990), overwintering through preimago (Papadopoulos et al. 1996, 1998; Israely et al. 1997; Katsoyannos et al. 1998), and summer migration from "nearby favorable areas" (Messenger and Flitters 1954).

The results of the different experiments in the present work are consistent and do not support the hypothesis that the Mediterranean fruit fly overwinters either as preimago or as adult in cold winter areas. Thus, migration from nearby favorable areas is the only option left. None of the infested apples, whether protected or unprotected from the rain, on sandy soil or Terra-Rosa, produced adults in the high altitude site (700 m), whereas at the lower site (400 m), flies emerged from such fruits. Our results coincide with previous studies suggesting that temperature is the most important factor affecting the Mediterranean fruit fly life history (Hill et al. 1988; Jessup et al. 1993; Vargas et al. 1996, 1997), followed by the effect of precipitation (Back and Pemberton 1918, Gjullin 1931, Rivnay 1950, Messenger and Flitters 1954). Examining Table 2 and its statistical analysis, we see that precipitation highly reduces adult emergence success.

The adult monitoring and fruit sampling in the mountains suggested a relationship between the times of adult captures and infested hosts detection, in that the first fly captured preceded infested hosts detection. We would expect the opposite relation if flies were local.

The fly release–recapture experiment demonstrated that under the local climate, adult Mediterranean fruit flies can survive for over a month during April–May and are capable of infesting local hosts such as loquat. Furthermore, released flies have demonstrated that even under low density they can be detected, as well as the infestation they cause. The theoretical degree-days calculation resulted in a gap of at least 4 wk between the expected day of adult emergence and actual captures (with an even greater gap if calculation begins before 15 December).

The Mediterranean fruit fly trapping data from the central and northern mountains of Israel show no evidence of any correlation between the quantity of apple-growing area and the size of the Mediterranean fruit fly summer population. It suggests that, in Israel at least, apples are not involved in the Mediterranean fruit fly's overwintering mechanism. The field results obtained by Papadopoulos et al. (1994) coincide with

Table 3. Dates on which flies emerged from infested apples that were collected on 22 November 2002

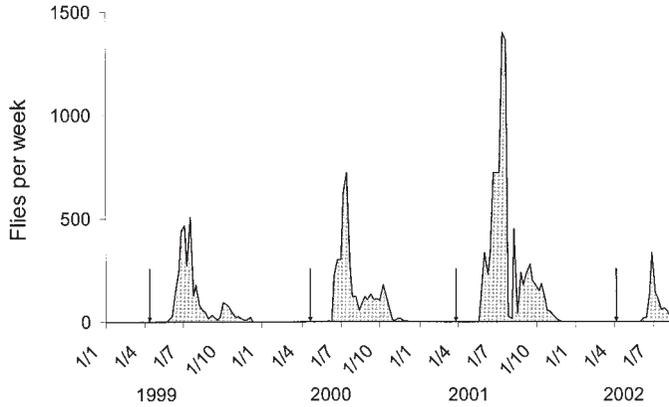| Altitude (m)	Accessibility to precipitation	Sandy soil	Terra-Rosa
700	Protected	No emergence	No emergence
	Unprotected	No emergence	No emergence
400	Protected	7 Jan. 2003–12 Mar. 2003	7 Jan. 2003–27 Mar. 2003
	Unprotected	15 Jan. 2003–8 Mar. 2003	15 Jan. 2003–5 Mar. 2003

Fig. 6. Total weekly catches of adult flies in a representative home garden in Zova (700-m altitude). Arrows indicate the expected dates of adult emergence, assuming oviposition on 15 December.

ours, in that flies were first observed after June. Their interpretation that a small, undetected fly population exists 2 to 3 months earlier seems to be a speculation based on their observations on maintenance of infested apples kept under favorable conditions that allow the flies to emerge until April. Our fly release–recapture experiment demonstrates that the sensitivity of monitoring is sufficient to detect a small population and therefore does not support the interpretations made by Papadopoulos et al. (1994, 1996, 2000, 2001).

If the data do not indicate that the Mediterranean fruit fly is local in cold winter areas, then the fly must be coming from elsewhere. We suggest, therefore, that the time has come to consider the migration hypothesis. Rivnay (1954) suggested that the Mediterranean fruit fly reinvades the mountains of Israel as summer begins and becomes extinct as winter commences. He speculated that the early summer flies that occur in the mountains migrate from the coastal plain of Israel where winter temperatures are milder. Rivnay based his speculation on two well-established details concerning the Mediterranean fruit fly in Israel. First, in the mountains flies are captured only from June to September (until the early 1950s) or December (current), and this is the only time when infested hosts are found there. Second, lowland flies are captured year-

round and exhibit a distinctive peak in the spring (Rivnay 1950). Fifty years later, the details on which Rivnay based his ideas are still valid. Furthermore, all studies conducted in cold winter areas report the absence of the Mediterranean fruit fly during the winter and spring (Bodenheimer 1951; Avidov and Harpaz 1969; Benfatto et al. 1989; Campos et al. 1989; Maelzer 1990; Michelakis 1992; Papadopoulos et al. 1996, 2001). "The common view suggests that lethal minimum temperatures (i.e., freezing) are the usual limiting factor" (Vera et al. 2002). However, subfreezing temperatures is a rare phenomenon in the current study area. For example, based on hourly data in the study area from 1998 to 2002, the average number of hours accumulated from January to May, inclusive, was 2,256 hours at temperature $T < 15°C$, 1,100 hours at $T < 10°C$, 92 h at $T < 5°C$, and only 3 h at $T < 0°C$. Hence, one may conclude that subfreezing temperature is probably not the reason for the Mediterranean fruit fly disappearance from the study area. Vera et al. (2002) suggest that the Mediterranean fruit fly colonization of cold winter areas is limited by "low maximum temperatures . . . denying it adequate thermal energy to sustain development." Their conclusion is supported by Messenger and Flitters' (1954) bioclimatic study, which found the fly to be highly sensitive to long periods of average temperatures below 13.9°C. In the
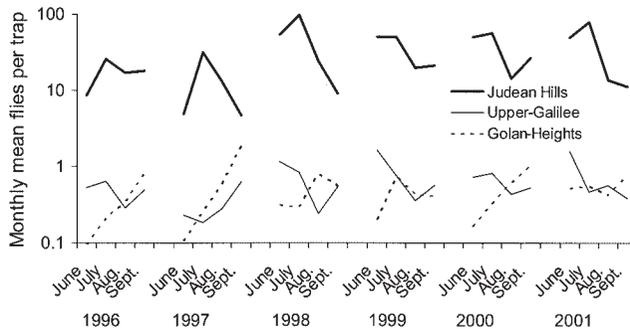

Fig. 7. Average monthly fly catches from June to September (1996–2001) in three mountainous areas of Israel.

central mountains of Israel, such temperatures occur for >2 mo in the winter.

In addition to temperature and precipitation, soil type was demonstrated to affect pupal survival. Eskafi and Fernandez (1990) showed that the strongest effect is caused by the combined action of high-bulk-density-saturated soil and low temperature (15°C). Such a combination caused the death of 98–99.8% of the larval and pupal population. These authors did not study the effect of temperatures lower than 15°C. Thus, a future study should concentrate on examining variables similar to those tested by Eskafi and Fernandez (1990), but at lower temperatures ranging from 0 to 15°C.

Further studies are required before one can establish whether the Mediterranean fruit fly overwinters in cold winter areas. This information is important for improving our understanding both of the Mediterranean fruit fly ecology and of required control practices. For example, under the current hypothesis (local overwintering) it is assumed that the Mediterranean fruit fly dispersion rate is low, and thus the mountain populations are isolated enough to develop flies more tolerant to cold. However, if the fly migrates annually then its dispersion rate is higher than previously expected. Current agricultural practice in the mountains includes spraying against the Mediterranean fruit fly before flies are captured in the summer, and again in the fall to reduce the population next year. If the fly migrates then these sprayings are unnecessary. Furthermore, this kind of ecological knowledge is highly important for mapping the geographical potential distribution of the Mediterranean fruit fly based on climate mapping (Gjullin 1931, Messenger and Flitters 1954, Carey 1996, Baker et al. 2000, Vera et al. 2002), and for better design of future area-wide-control campaigns. The spatial theoretical distribution mapping of invading Mediterranean fruit fly suggested by Carey (1996) for California assumes that the fly can overwinter in areas with subzero temperatures, such as northern Greece and the Judean Hills in Israel. Under our findings, these maps should be reevaluated.

Acknowledgments

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Effect of Combined Insecticide Sprays and Sanitation Techniques on Population Dynamics of *Ceratitis capitata* (Diptera: Tephritidae) in the Central Mountains of Israel

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ABSTRACT We conducted an environmental manipulation study over a 7-km^2 area to examine the effect of different control levels on the population dynamics of *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) in the central mountains of Israel. Adult male monitoring was carried out from spring to fall during 1988–1991 and year-round from 1994 to 2001. From 1995 to 1997, we manipulated the study area, imposing different levels of control by using a combination of insecticide sprays, tree pruning and removal, and fruit stripping. In the years preceding the manipulation, population dynamics was characterized by a peak summer population size in June–July, followed by a population decrease in August, leading to an early fall peak in September–October. If flies overwinter locally, we expected the intensive control to decrease the early summer population after the control. If flies do not overwinter locally, the control and sanitation activities should not decrease the population level in the following summer. During the entire period discussed, no flies were captured between January and May. The first appearance was recorded in late May or early June, reaching a peak in July. Regardless of control level and extent, the early summer peak remained unchanged during the entire study period, whereas the later fall peak decreased as host density decreased. We suggest that the first peak is the result of a seasonal reinvading population, whereas the later peak is governed by host availability and multiplication of the invading flies. The meaning and possible practical implications of our findings are discussed.

KEY WORDS *Ceratitis capitata*, overwintering, cold resistance, pest management, sanitation

AN UNDERSTANDING OF LIFE HISTORY strategy is fundamental in ecological studies (Denno and Dingle 1981). Every living organism must be prepared to undergo harsh, hostile, and unpredictable environmental conditions during its lifetime. Unfavorable conditions may result from seasonality, global climate changes, or change of habitat, as with invading species (Gates 1993). Such conditions include lack of food, excessive or insufficient moisture, and extreme temperatures. Invasive species that colonize new, unpredictable environments are either preadapted to them or undergo adaptation to avoid extinction (see Carey 1993 for phases in invasion biology). Through adaptation, invasive species may respond to an unpredictable environment by means of behavior, physiological, or morphological adjustments (Geist 1978). Studying such strategies is of theoretical and practical importance, particularly for Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). *C. capitata* is of tropical origin, but throughout the 20th century it has invaded the temperate region. In its original habitat of tropical east Africa (Headrick and Goeden 1996), *C. capitata* generally did not have to confront extreme effects of temperature, long duration of off-season, or lack of hosts during part of the year. However, it had to deal with high amounts of rain. Monophagous, univoltine fruit fly species such as *Rhagoletis pomonella* (Walsh), *Rhagoletis cerasi* (L.), or *Urophora jaceana* (Hering) are expected to emerge next to their host just when the following year's fruit is ready and may produce several successive generations on the same plant. Thus, they disperse over a small area (Aluja 1993). In contrast, polyphagous, multivoltine, nondiapausing species such as *Bactrocera tryoni* (Froggatt), *Dacus cucurbitae* (Coquillett), *Dacus dorsalis* (Hendel), and *Anastrepha ludens* (Loew) are strong fliers and are highly mobile (Aluja 1993). They emerge into an environment where local hosts may have already been exhausted and thus need to search for alternative suitable hosts for their progeny. Under such circumstances, the ability to fly long distances is a clear advantage, as for *B. tryoni* (Fletcher 1973). The polyphagous *C. capitata* is generally believed to be a short-distance flier (Hagen et al. 1981, Plant and Cunningham 1991). However, wind-assisted long-distance

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flight was demonstrated by Bateman (1972) and Goldenberg et al. (1975). The nondiapausing, multivoltine features of *C. capitata* (Bateman 1972) make it highly suitable for life in the tropics. The same features make it difficult to acclimatize to temperate regions where the environment is governed by seasonality, including lack of hosts for long periods. Nonetheless, during the past 100 yr, *C. capitata* has expanded its habitat far beyond the African tropics into all the continents and into the temperate zone, as far as 41° N (Fischer-Colbrie and Busch-Petersen 1989). At its northernmost area, as well as in other cold-winter regions, it is recorded only during the summer and fall (Bodenheimer 1951, Israely et al. 1997, Papadopoulos et al. 2001b). Where and how *C. capitata* survives the winter and spring is still disputed.

C. capitata is thought to have no cold-tolerance mechanism or any kind of diapause to carry it through cold periods with possible subzero temperatures (Christenson and Foote 1960). Nevertheless, some investigators have suggested the adult is the overwintering stage (Carante and Lemaitre 1990). Others indicate the pupa (Katsoyannos et al. 1998) or larva (Papadopoulos et al. 1998) is the overwintering stage in cold areas. This would be possible if *C. capitata* has become acclimatized to cold areas (Hagen et al. 1981, Meats 1989a) and developed strains that survive subzero temperatures (Papadopoulos et al. 1996), as with the Australian fruit fly *B. tryoni* (Bateman 1967, Meats 1989b). In Israel, Rivnay (1954) suggested that *C. capitata* does not overwinter in cold regions but reinvades the highlands from warmer adjacent areas seasonally. Until recently that theory has not been tested. However, a new study by Israely et al. (2004) supports Rivnay's idea. These authors examined whether *C. capitata* overwinters or reinvades the cold winter areas, by using numerous techniques, the results of which supported the reinvasion hypothesis. The present article further strengthens this hypothesis. This was achieved by studying the quantitative effects of a combination of insecticide spray and various sanitation techniques on *C. capitata* population dynamics in cold-winter areas. The rationale behind this approach was that if *C. capitata* overwinters locally, then its population should decrease after chemical control and elimination of its hosts, in particular overwintering hosts such as late apple (*Malus* spp.) varieties. However, if the fly reinvades annually then strict control of late summer hosts in any year should not affect the following year's summer population size. To compare these hypotheses we carried out a sanitation operation combining insecticide spray and host elimination, and recorded *C. capitata* trappings before and after the operation. The ratio of summer to preceding fall trappings was compared with the corresponding ratios for years in which there had not been host elimination. We then computed *P* values under the null hypothesis of overwintering versus the alternative hypothesis of reinvasion. Due to the size of the study area, it was not feasible to conduct a classical replicated field experiment, and hence our statistical results should not be interpreted as "statistical proof"

Table 1. Main noncommercial hosts in the Kibbutz Zova, Israel, study area during 1997 in which control and sanitation treatments were used to reduce *C. capitata* populations

Host	No. trees	Treatment	
		Wild	Residential
Fig	651	Pruning	Pruning/spray
Grapes	>100	Not treated	Spray/fruit stripping
Prickly pear	≈100	Not treated	Not treated
Plum	46	Pruning	Spray/fruit stripping
Pear	34	Pruning	Pruning/spray
Apple	29	Pruning	Spray/fruit stripping
Apricot	28	Fruit stripping	Pruning
Loquat	22	None present	Not treated
Citrus spp.	27	Not treated	Spray
Cherry	17	Not treated	Spray
Nectarine	5	None present	Spray/fruit stripping
Peach	5	None present	Spray/fruit stripping

of the reinvasion hypothesis, but rather as giving additional ecological evidence for comparing the two models of *C. capitata* winter population dynamics (Hargrove and Pickering 1992).

Materials and Methods

Observational Period, Site, Climate, and Hosts. The study took place in the surroundings of Kibbutz Zova from 1994 to 2001. The study area covered a 2 by 3.5-km rectangle located in the central mountains of Israel at the Judean Hills west of Jerusalem, 600–750 m above sea level (31° 51′ 08″ N, 35° 05′ 14″ E). The climate is Mediterranean with hot, dry summers and wet, cold winters. The annual average precipitation is 600 mm, all falling between December and April. During the winter, temperatures may fall below zero, and occasionally it may snow; for further climatic information, see Israely et al. (1997).

Kibbutz Zova is located in the center of the study area (Israely et al. 2004). The settlement is surrounded by forests of allepo pine, *Pinus halepensis* Miller; cypress, *Cupressus* sp.; and typical Mediterranean vegetation such as sumac, *Rhus* spp.; pistachio, *Pistacia lentiscus* L.; oak, *Quercus* spp.; eucalyptus, *Eucalyptus* spp.; carob, *Ceratonia siliqua* L.; prickly pear, *Opuntia* spp.; almond, *Prunus amygdalus* Batsch; fig, *Ficus carica* L.; olive, *Olea europaea* L.; pomegranate, *Punica granatum* L.; and grape, *Vitis vinifera* L. The settlement also is surrounded by commercial plots of nectarine, *Persica vulgaris* Miller (3 ha); English walnut, *Juglans regia* L. (5 ha); sweet cherry, *Prunus avium* L. (0.7 ha); apple, *Pyrus malus* L. (21 ha); and pear, *Pyrus communis* L. (2.2 ha). All plot sizes are for 1997. The residential area teems with diverse hosts such as plum, *Prunus domestica* L.; pear; apple; apricot, *Prunus armeniaca* L.; citrus, *Citrus* spp.; loquat, *Eriobotrya japonica* Lindley; cherry, *Prunus cerasus* L. and *P. avium* L.; nectarine, peaches; and feijoa, *Feijoa sellowiana* O. Berg. Aside from the commercial orchards, figs are the most important host in the wild, with apricot and loquat in the residential area. This is because of their relatively high number compared with other hosts (Table 1), as well as the very high density of fruit that

each tree bears. During the study period, no major changes occurred in the host situation in and around the study area, aside from what is discussed below. Accurate identification of the flora was done according to Feinbrun-Dothan and Danin (1991).

First Control Operation: Commercial Apple Plots. Because apples, particularly late varieties (e.g., Golden Delicious and Granny Smith), were assumed to be a major overwintering host (Israely et al. 1997; Papadopoulos et al. 1996, 2002), we chose to study the effect of insecticidal sprays and sanitation in such plots. From 1995 to 1997, three steps were taken to ensure that commercial plots in the study area were not the source of the summer population. First, before picking (May–August), orchards were intensively sprayed. Two to 3 mo before picking, plots were sprayed from the ground once a week with a cover spray containing 0.1% dimethoate (Makhteshim Ltd., Be'er-Sheva, Israel) at a rate of 10 m^3/ha. A month before picking, as well as during picking (August–October), plots were sprayed twice a week by using a mixture of 10% malathion 25 WP (Makhteshim Ltd.) and 10% bominal, a protein hydrolysate bait (Luithlen Werke GmbH & Co. KG., Andernach, Germany). Second, after picking (October), unpicked fruits left on trees were collected and left on the ground to enhance their decomposition, ensuring that fruit decay was achieved within 1–3 wk (and thus at least 8 wk before winter arrived). Third, during November plots were revisited, and fruit found on trees or on the ground was collected in plastic bags and put into garbage containers, which were then buried some 20-km distant from the research area.

Second Control Operation: Entire Study Area. In 1997, an intensive sanitation program was conducted throughout the entire study area for all hosts in the residential area and commercial plots, as well as for wild hosts. The sanitation program had two major stages. First, a complete *C. capitata* host census and mapping were conducted and later incorporated into a geographic information system (GIS) database. Second, main hosts in the study area (primarily fig, apricot, nectarine, apple, pear, *Citrus* spp., and plum) were treated in one of the following ways: 1) felling or pruning such that the tree would not bear fruit for at least 1 yr; 2) fruit stripping; or 3) spraying such that trees bearing hosts that were not stripped were treated with bait or cover spray, as described above (Table 1).

Hosts that ripened between January and mid-May (winter and spring), as well as those that from our previous experience were not usually infested, were not treated (e.g., early cherry, loquat, and winter citrus). The same was true for summer hosts that were previously found not to be infested or infested at a very low rate (e.g., prickly pear, vegetables, and walnut). For the sake of quality control and environmental reasons, we preferred using pruning and felling, host stripping, and collection techniques when possible because they are durable compared with insecticide sprays, which protect fruit for no more then a single week and hence require repeated treatments. In general, commercial hosts were cover-sprayed and

picked. After picking, the remaining fruit was collected (October–December 1996); wild hosts outside the residential area were pruned (January–April 1997); and in the residential area, ≈50% of the hosts were pruned (January–April 1997), 20% were stripped (April–May 1997), and 30% were sprayed (throughout the summer) by using the same bait mixture described above. Hosts were pruned in the residential area unless the owner objected, in which case they were stripped. If both methods were unacceptable to the owner, the hosts were sprayed. As an extra precaution, and to ensure that apple plots would not harbor an overwintering population, the major portion (12 ha) of late-ripening apple varieties (i.e., Golden Delicious and Granny Smith) were sprayed weekly from late May (2 wk before flies occurred that year) until the end of picking in October.

Sampling and Treatment Scheme. Traps were deployed throughout the study area on host trees (Table 1), with some on nonhosts (e.g., pine, cypress, and pistachio). These hosts included trees that did not undergo sanitation during the first operation, which was carried out only in apple orchards. Hosts that are more common in the study area (e.g., fig, apricot, and apple) received a relatively higher number of traps than others (e.g., grapes and plum). Aside from a few cases, traps were located at least 50 m from one another; for further details see Israely et al. (1997). Adult males were monitored and recorded on a weekly basis, year-round, for five consecutive years, from 1994 to 1999. For monitoring, we used Nadel-type traps, baited with trimedlure. This type of trap is standard for *C. capitata* monitoring in Israel (Roessler 1988). The number of traps deployed each year was 70, 132, 133, 123, 165, and 147, respectively. In addition, in years before and after the main study period (i.e., 1988–1991 and 2000–2001), we used a much smaller number of traps, i.e., 11, 12, 9, 8, 20, and 20, respectively. During 1988–1991, flies were monitored from May through September and year-around during 2000–2001.

Statistical Analyses. We analyzed the data from 1994 through 1999, when relatively large numbers of traps were deployed. If *C. capitata* overwinters locally, then the reduced potential population pool in the fall of a control year should give a corresponding reduction in the following summer population. However, if the fly migrates, then the summer population size would be unaffected, because it consists of flies arriving from nonsanitized regions. Thus, due to the fall population reduction, under the reinvasion hypothesis the summer-to-fall ratio would be larger than expected. Because the summer-to-fall ratio depends on a number of factors, which may vary from year to year (e.g., survival rates under the overwintering hypothesis; and uprooting of orchards, planting, and different levels of picking in the source area under the reinvasion hypothesis), we compared the ratios for the control years (1996/1995 and 1997/1996 for the first operation in commercial apple plots; 1999/1998 for the second operation, in the entire study area) with the corresponding ratios for years in which there were no control operations.
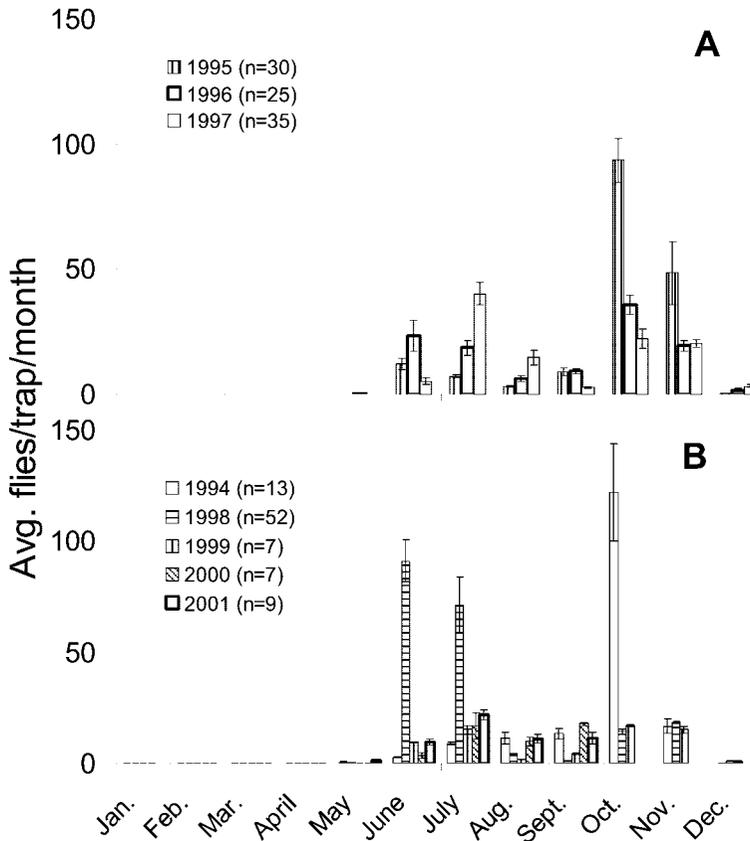
Fig. 1. Monthly average ± SE number of *C. capitata* caught, per trap, in apple orchards during 1994–2001 in Kibbutz Zova, Israel. (A) Fly trapping under intensive control and sanitation campaign. (B) Fly trapping under regular control. From 1995 to 1997 fruits remaining after harvest (October–December) were collected and destroyed.

Except for one case where several traps were suspended in a single home garden in the residential area, the traps were placed sufficiently distant (at least 50 m) from one another to assume independence among traps. For each trap, successive weekly counts were averaged because of temporal correlation, and analyses were based on these time averages. There was no reason to assume year-to-year dependence for a given trap. Each trap's fall weekly average was based on October–November, to ensure independence from its June–July summer average. All time averages were logarithmically (base 10) transformed to improve normality; thus, the summer-to-fall ratios translate into summer–fall differences. Even after the logarithmic transformation, the variances for the groups being compared could not be assumed constant. In view of this, and the differing numbers of traps per group, Welch's approximation was used in computing P values. To account for multiple inference, Bonferroni's inequality was used to assess significance of the P values.

Logistic, economic, and social constraints precluded conducting a study of this size as a designed experiment, in which case we would have corrected for year-to-year variability by conducting the sani-

tation operations in several years, as well as obtaining trapping information for untreated hosts during the sanitation years to provide a control group. Therefore, our statistical results should be treated with caution.

Results

Combined Sprays and Sanitation in Commercial Plots. During 1994–1996 the trapping pattern in apple orchards remained the same: a small early summer peak in June–July and a large late fall peak in October (Fig. 1). These results are consistent with a previous study (Israely et al. 1997), together with trapping data from 1988 to 1991 (Fig. 2), which showed the following characteristic pattern for the study area: catches begin in June and peak sometime in July—August, with a subsequent fall peak that begins to increase in September.

Combined Sprays and Sanitation in Entire Study Area. Figure 3 exhibits weekly trapping averages for the three types of hosts or habitats for 1994–1999. Control was done for a year, from October 1996 to October 1997. In the period preceding the intensive control, the curves in the entire area were similar to
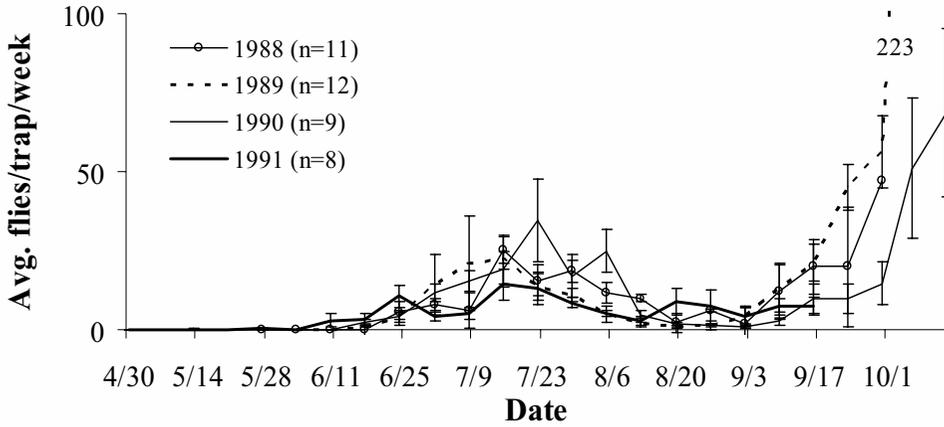
Fig. 2. Average ± SE number of flies caught (per trap) in apple orchards during 1988–1991 in Kibbutz Zova, Israel.

those in the apple orchards, characterized by a summer peak followed by a much larger fall peak (Fig. 3a–c). In 1997, during the extensive control and sanitation campaign, a large population increase during July in apple orchards and home gardens was detected; however, there is barely such a peak in figs (Fig. 3d–f). The fall peak in 1997 has almost disappeared from the figs and home gardens, whereas remaining in apple plots. During 1998, the year following the extensive control, the curves look different: all three hosts or habitat types demonstrate a very large peak in July, followed by a minor peak in October (Fig. 3g–i). The effect of the host felling and pruning is clearly seen 2 yr later (1999) in the small October peak in home gardens (Fig. 3l). In contrast, fig trees

demonstrate a remarkable degree of recovery, showing approximately the same population size in the October peak as before the felling (i.e., 1994–1996) (Fig. 3k). Because commercial apple orchards did not receive any special treatment of felling or pruning, we did not expect any long-term effect on its fly population (Fig. 3j). From 1994 to 1999, the infestation rate in commercial apple plots of late varieties (i.e., Golden Delicious and Granny Smith) was extremely low and did not exceed 0.1%. An exception was 1998, when one Golden Delicious plot was heavily infested ($\approx$30%). However, in this plot, as in others, eggs and larvae died within the host and did not complete development due to the intensive insecticide spray after infestations.
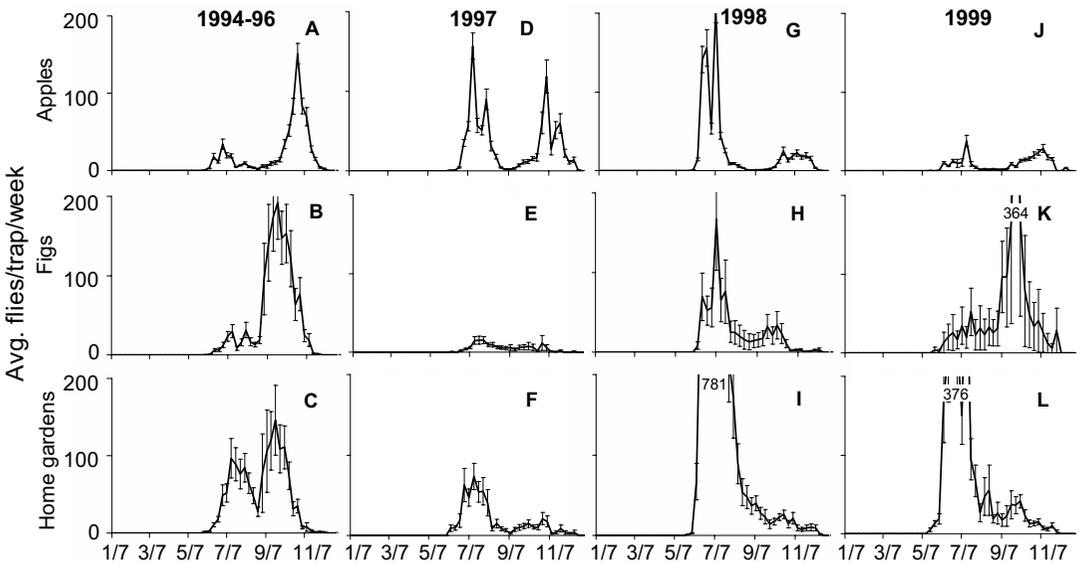

Fig. 3. *C. capitata* weekly mean ± SE catches per trap in apple orchards, wild figs, and residential home-gardens before (1994–1996), during (1997), and after (1998, 1999) the combined insecticide spraying and sanitation operation in Kibbutz Zova, Israel.

Table 2. Summer (June–July) and fall (Octover–November) weekly mean number of *C. capitata* captured per trap (logarithmic units) in commercial (apples), wild (figs), and residential (gardens) hosts

Season	Yr	Apples			Figs			Gardens		
		No. traps	Mean	SD	No. traps	Mean	SD	No. traps	Mean	SD
Fall	1994	13	1.84	0.19	6	1.23	1.02	4	1.82	0.32
	1995	17	1.69	0.55	18	1.36	0.87	4	1.75	0.76
	1996	16	1.22	0.62	7	1.25	0.83	53	0.75	0.49
	1997	33	1.18	0.34	9	0.31	0.57	11	0.74	0.66
	1998	46	1.00	0.43	6	0.56	0.69	11	1.05	0.38
	1999	37	1.01	0.35	2	1.47	1.08	5	1.30	0.16
Summer	1994	3	0.66	0.17	3	0.65	0.70	4	1.12	0.65
	1995	17	0.86	0.26	17	0.78	0.55	5	1.46	0.92
	1996	21	1.12	0.42	7	0.84	0.59	31	1.19	0.49
	1997	28	1.25	0.30	10	0.67	0.35	11	1.33	0.64
	1998	48	1.79	0.32	9	1.50	0.57	10	2.34	0.41
	1999	54	0.86	0.36	4	0.99	0.73	7	2.32	0.19

Comparison of Overwintering and Reinvasion Hypotheses. Table 2 provides summary statistics, by year, for the logarithms of the average weekly summer trappings (over 9 wk in June–July) and fall trappings (over 9 wk in October–November). Table 3 presents the summer-to-fall ratios, in original units, corresponding to differences of the means given in Table 2 (Table 3 does not contain standard deviations as the statistical analysis is based on the logarithmic data of Table 2). For example, the summer 1998–fall 1997 difference of 1.79–1.18 = 0.61 for apples in Table 2 translates into the ratio 4.09 in Table 3; i.e., the estimated expected number of flies per trap in summer 1998 was ≈4 times the number in fall 1997.

As discussed above, if *C. capitata* overwinters locally, then we would expect similar summer-to-fall ratios for all years, including those when the control operations were applied. However, if the fly migrates, then we would expect larger summer-to-fall ratios for the years of the control operations. We thus compared the ratios for control years with those for noncontrol years. Because the analysis is in logarithmic units, we contrast summer–fall differences of the control year means in Table 2 with the differences for noncontrol years.

Consider first the control operation for commercial apples in 1995 and 1996. The corresponding ratios, underlined in Table 3, are both larger than the ratio for 1994; but only the 1996 ratio is larger than the ratio for the other noncontrol year, 1998. Table 4 gives the corresponding mean contrasts, together

with their *P* values. The *P* values are computed under the null hypothesis that the underlying contrast is zero (corresponding to the overwintering hypothesis), whereas the alternative hypothesis is that the underlying contrast is positive, supporting the reinvasion model. Because of the multiple inference involved, each *P* value is compared with 0.05/4 = 0.0125 to assess significance. We see that the results for both control years are significant for the reinvasion hypothesis, compared with 1994, but that neither is significant compared with 1998. The results of the first sanitation operation are thus inconclusive regarding the two hypotheses.

Next, consider the major control operation carried out for all hosts in 1997. The summer-to-fall ratios, exhibited in bold in Table 3, are larger (often by an order of magnitude) than the ratios for the noncontrol years. In view of the inconclusive results for the control operation in apple orchards, we consider their summer 1996/fall 1995 ratio as for a "noncontrol" year with respect to the major control operation. The mean contrasts and their *P* values, analogous to Table 4 for the first control operation, are given in Table 5. We see that the comparisons with 1998 for figs and home gardens, although small, are not significant, whereas all the remaining contrasts are highly significant. Thus, the second control operation gives very strong support to the reinvasion hypothesis.

Table 3. Estimated summer-to-preceding-fall ratios of weekly number of *C. capitata* captured per trap (original units) in commercial (apples), wild (figs), and residential (gardens) hosts

Summer/fall		Apples	Figs	Gardens
1995	1994	0.10	0.35	0.44
1996	1995	0.27	0.30	0.28
1997	1996	1.06	0.26	3.84
1998	1997	**4.09**	**15.13**	**40.45**
1999	1998	0.73	2.66	18.37

Entries are ratios between 10 raised to the power of the corresponding means in Table 2. Results for year of second control operation are in bold; results for years of first control operation are underlined.

Table 4. Comparisons of summer (S) (June–July) and fall (F) (October–November) differences in mean number of *C. capitata* captured per trap (Table 2; logarithmic units) for control and sanitation years in commercial apple plots (1996/1995, 1997/1996), with summer–fall differences for noncontrol and sanitation years (1995/1994, 1999/1998)

Comparison	Apples	
	Mean	*P*
(S96–F95)–(S95–F94)	0.41	0.02
(S96–F95)–(S99–F98)	−0.44	0.99
(S97–F96)–(S95–F94)	1.01	<0.0001*
(S97–F96)–(S99–F98)	0.16	0.19

Entries are mean difference comparisons and *P* values under the null hypothesis that flies overwinter locally. Asterisk (*) indicates significant difference under multiple inference (*P* must be <(0.05)/4; see *Materials and Methods*, Statistical Analyses).

Table 5.   Comparisons of summer (S) (June–July) − fall (F) (October–November) difference in mean number of *C. capitata* captured per trap (Table 2; logarithmic units) for year of second control and sanitation operation (1998/1997), with summer–fall differences for noncontrol and sanitation years in commercial (apples), wild (figs), and residential (gardens) hosts

Comparison	Apples		Figs		Home gardens	
	Mean	P	Mean	P	Mean	P
(S98–F97)–(S95–F94)	1.60	<0.0001*	1.63	0.0018*	1.97	0.0005*
(S98–F97)–(S96–F95)	1.18	<0.0001*	1.71	0.0001*	2.16	<0.0001*
(S98–F97)–(S99–F98)	0.75	<0.0001*	0.76	0.08	0.34	0.11

Entries are mean difference comparisons and *P* values under the null hypothesis that flies overwinter locally. Asterisk (*) indicates significant difference under multiple inference (*P* must be <(0.05)/9; see *Materials and Methods*, Statistical Analyses).

Discussion

Our results show the following. First, before different levels of control were imposed, the population dynamics was largely predictable, with a small summer peak followed by a relatively large fall peak. These two peaks do not represent two successive generations, because several generations were observed to develop annually in the central mountains (Avidov 1961). Thus, the population fluctuations (July and October) reflect seasonal fruit availability (Israely et al. 1997, 2004), as with *B. tryoni* (Drew and Hooper 1983). Second, imposing different levels of control over the entire study area did not influence the summer peak but strongly reduced the fall peak. Third, strict control procedures of apple orchards affected neither the summer nor the fall peak, ruling out the possibility that apples serve as an overwintering host. These results further support the study of Israely et al. (2004), which suggested that *C. capitata* does not overwinter in the central mountains of Israel, but rather reinvades them annually.

The overwintering strategy of *C. capitata* is central to its ecology, and a more comprehensive understanding of its biology and physiological characteristics will aid efforts to control it. Understanding *C. capitata* ecology is another step toward gaining more knowledge of the phenomenon of tropically originating insects that invade and rapidly establish themselves in temperate regions.

Until now, no study has suggested an approach that would permit a full understanding of *C. capitata* overwintering dilemma. Rivnay (1954) suggested that *C. capitata* does not overwinter in the highlands of Israel but reinvades them from the lowlands as summer begins. According to Rivnay (1954), population decreases in the lowlands during June–August might explain the simultaneous population increases in the highlands. However, Rivnay (1954) did not support the ideas experimentally: the ideas were based on flies not being trapped in the highlands during the winter and fall and on early hosts that ripen before June not being infested. However, Papadopoulos et al. (1996) suggested that *C. capitata* does overwinter in cold areas with subzero temperatures. According to their study, *C. capitata* larvae could survive low temperatures for long durations, even in the cold area of northern Greece, and emerge as adults in the following spring (i.e., April–May). However, they did not detect any adults earlier than June–August. Papado-

poulos et al. (2001a) expected flies to infest spring and early summer hosts, but they detected infestation only at the end of June. Thus, their laboratory observations were not supported by their field observations. With no infested hosts and no adults monitored during the winter, spring, and early summer, the conclusions of Papadopoulos et al. (1996, 2001a) seem unsubstantiated. They explain this discrepancy in the limited ability of the trapping system to detect very low populations. Israely et al. (2004), who favor the reinvasion hypothesis, demonstrated that a small number of flies that were released in the mountains in the late winter were recaptured in high percentages by using a similar trapping system. Israely et al. (2005a, b) later demonstrate the seasonal reinvasion of flies from the lowland to the highland, as predicted by Rivnay (1954).

One reason for the difficulty in understanding the *C. capitata* overwintering mechanism is that the characteristic pattern of a summer peak beginning in June, followed by a larger fall peak (Israely et al. 1997; Figs. 1–2), is consistent both with local overwintering (because apples are the main host in the study area, we would expect overwintering flies would be expected to emerge no later than June) and with reinvasion (it would take some time for the flies to arrive from warmer areas). Under strict control, different trapping patterns are expected depending on *C. capitata* winter population dynamics. Thus, using environmental manipulations, we may examine the two alternative hypotheses (a local overwintering population versus annual reinvasion) by comparing their predicted results with those actually observed in the field.

Our first manipulation involved host control and sanitation inside commercial orchards, applied by spraying before picking, followed by fruit collection and destruction after picking. This study was important in light of previous experiments suggesting apples as the bridging host used by the preimago stages of *C. capitata* to overwinter in cold regions. If *C. capitata* overwinters locally, then the reduced potential population pool in fall should give a corresponding reduction in the following summer population. However, if *C. capitata* migrates, then the summer population size would be unaffected, because it consists of flies arriving from nonsanitized regions. Thus, because of the population reduction in fall, under the reinvasion hypothesis the ratio of the following summer trappings to those for fall would be larger than expected. Because the summer-to-fall ratio depends

on several factors, which may vary from year to year (e.g., survival rates under the overwintering hypothesis, uprooting of orchards, planting, different levels of picking in the source area under the reinvasion hypothesis), we compared the summer-to-fall ratios for the control years (1996/1995 and 1997/1996) with the ratios for the noncontrol years (1995/1994 and 1999/1998). The results, in Table 4, are ambiguous; thus the first manipulation did not give clear support to either of the overwintering hypotheses.

Our second environmental manipulation, conducted during 1997, included thorough control and sanitation of the entire study area. It is estimated that this procedure caused the loss of 90–95% of the potential local hosts for *C. capitata*, thereby resulting in a very small population in fall 1997. This occurred (Fig. 3) for each of the three host categories in the study area (apple, fig, and home gardens). Using the same rationale as with the first environmental manipulation, to evaluate the overwintering hypotheses, we compared the 1998/1997 summer-to-fall ratios, for the different hosts, with the ratios for the noncontrol years. The results, in Table 5, very strongly support the reinvasion hypothesis. Of equal, if not greater, importance than the *P* values are the orders of magnitude of the comparisons: translating the significant means in Table 5 back into original units, the 1998/1997 ratio was between $10^{0.75} = 6$ and $10^{2.16} = 145$ times larger than the noncontrol ratios, depending on the host and year.

We remark that in 1997, in spite of the drastic control measures taken, the June–July peak for apple orchards was even larger than usual (Fig. 3d). We suggest that this increase had no connection with our environmental manipulation that year but may have been a result of agricultural changes at the fly's overwintering sites ("source area"), which is the lowland according to Israely et al. (2005a). For example, a change in picking quality instructions of *Citrus* spp. (the main overwintering hosts) in the lowland will cause a change in fruit quantity remaining on trees after picking. The more *Citrus* spp. left on trees in the spring, the larger is the potential invading population to the highland.

Although we have attempted to correct for confounding factors in our statistical analysis, our manipulations should be interpreted as "quasi-experiments," i.e., experiments that assume there would have been no changes in a region if no treatment had been applied or if the treatment had no effect (Hargrove and Pickering 1992). We suggest that this drawback is compensated for by the scope, both geographical and temporal, of the study: >10 yr of population monitoring was conducted in an area of 7 km². Moreover, we emphasize that data obtained during a 7-yr period preceding the extensive control by a combination of insecticide sprays, and sanitation techniques during 1997, showed a consistent pattern of small summer peaks following large fall ones. In contrast, after the extensive control of 1997 the situation was reversed, with the summer-to-fall ratios for each of the host types ranging from 6 to 145 times as large as in previous

years. Interpretations of statistical significance aside, we believe this result very strongly supports the reinvasion hypothesis.

Our results further support the study of Israely et al. (2004) and suggest that *C. capitata* has not yet become adapted or gone through evolutionary steps to adjust to cold winter temperate regions; rather, like other tropical fruit flies, it simply uses what it naturally owns: a rapid capacity for reproduction when conditions are favorable and an ability to migrate (see Johnson 1969 and Kennedy 1986 for definition of migration) to new sites when population size is over the carrying capacity (Bateman 1976). Using that strategy, *C. capitata* survives the winter in the safety of the relatively warm regions, while using the warmer seasons for reinvasions. The same strategy is believed to be used by other multivoltine tropical and subtropical species. Fletcher (1973) suggested that *B. tryoni*, like "other organisms that breed in discrete and temporary habitats . . . evolved a well-developed power of dispersal" that facilitates its seasonal migration into remote and discrete sites in the inland of Australia, whereas it overwinters in its natural habitat of subtropical rain forests along the eastern coast. Drew and Hooper (1983) suggested that the increase in capture of some Australian *Dacus* spp. "at the higher altitude . . . probably represents an influx of flies from lower altitude. These immigrant flies then breed in native and cultivated fruits in the November-January (i.e., Australian summer) period before populations start to decline due to a decline in host fruit and decreasing temperatures." Based on the current study and previous ones (Israely et al. 2004, 2005a), we suggest that the same mechanism maintains *C. capitata* population in the cold regions of Israel where it is found throughout the summer.

If *C. capitata* does not overwinter in cold regions (Israely et al. 2004, 2005a, b), this knowledge should be applied in the study of its ecology. For example, *C. capitata* population ecology should be studied on a much larger scale than previously. Further studies should be performed to determine the different climatic factors responsible for the inability of *C. capitata* to overwinter in cold areas. Once this has been done, risk assessment maps incorporating *C. capitata* phenology with climatic data can be produced.

The relevance of our findings should be further studied in other temperate locations where *C. capitata* presents similar ecological characteristics. If indeed the fly is sensitive to low temperatures and is dependent upon annual reinvasion to cold regions, then this information can be used for the development of areawide control strategies. An additional implication is that the best time to start an areawide control program is in the winter, when flies are confined to limited areas. If such a control program is launched at the end of the winter, then it only needs to deal with a small fly population existing in the warmer areas. Finally, the significance of this finding to areawide control projects cannot be underestimated. Areawide control projects should concentrate on preventing the flies from reestablishing new populations in cold regions

from which they disappear during the winter, rather than attempting to eliminate them after they have already reestablished.

Acknowledgments

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Spatiotemporal Distribution Patterns of Mediterranean Fruit Fly (Diptera: Tephritidae) in the Central Region of Israel

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ABSTRACT   The geographical distribution of Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), is limited to relatively warm regions and does not cross the 41° north latitude. A recent study has demonstrated that, in contrast to the earlier suggested hypothesis, that Mediterranean fruit fly can survive the winter in relatively cold areas, it does not overwinter in such areas but reinvades them annually from adjacent warmer sites. In the present work, we use a large-scale spatial approach to describe the spatiotemporal dynamics of Mediterranean fruit fly in a large heterogeneous landscape as well as discuss the consequences of such dynamics for basic research and control practices. During a 2-yr period (2000–2001), over the central part of Israel (6,875 km²), adult males were monitored and recorded weekly by using Steiner-like traps. Data obtained were incorporated into a geographic information system to produce weekly distribution maps of *C. capitata* within the study area. The patterns of change in population sizes through time were consistent in both years, suggesting that *C. capitata* overwinters along the coastal plain and the Jordan Valley. Reinvasion to the higher altitudes is followed by a population increase in the warmer, lower altitudes, during the spring and early summer. By midsummer, flies were found at all sites within the study area. However, flies started disappearing from the high-altitude areas during fall and were absent from these areas during winter. We suggest that understanding such spatiotemporal dynamics has far-reaching consequences for future basic research as well as control and eradication programs.

KEY WORDS   *Ceratitis capitata*, overwintering, spatial patterns, population distribution pattern, invasion

THE DISTRIBUTION AND POPULATION dynamics of Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), have attracted much attention in previous years due to its major damage to agricultural crops worldwide (Gjullin 1931, Liquido et al. 1991, Vera et al. 2002). In the Mediterranean region, several researchers argued that, despite its tropical origin, local Mediterranean fruit fly populations have been adapted to cope with the cold temperatures prevail in high altitudes as an explanation to their presence there (Papadopoulos et al. 1996, 1998, 2001b). However, empirical support for that argument was not evident. A recent study conducted in the central mountain region of Israel (Israely et al. 2004) showed that Mediterranean fruit fly did not overwinter there, but rather, as it has been shown previously (Bodenheimer 1951, Avidov 1961), in the coastal plain and the inner valleys of Israel, where winters are warmer. Israely et al. (2004) suggested that Mediterranean fruit fly populations rein-

vaded the mountains with the onset of summer. Fruit flies survival mechanism through summer reinvasion from warmer sites has previously been suggested for some *Dacus* species in cold areas of Australia (Drew and Hooper 1983).

In spite of the variable conditions under which Mediterranean fruit fly maintains consistent populations, its ecology and biology have been studied mainly on small scales (e.g., cages, a tree, or a single field), or on rare occasions, on slightly larger scales (10–100 km²) (Prokopy and Hendrichs 1979; Carey 1982, Harris and Lee 1986, 1987, 1989; Vargas and Nishida 1989; Hendrichs and Hendrichs 1990; Michelakis 1992; Israely et al. 1997; Warburg and Yuval 1997; Papadopoulos et al. 2001a, b). At a large scale, it is likely that the fly's population combines physiological, genetic, and behavioral adaptations of the coastal and mountain populations. Therefore, a large-scale study, covering both areas interconnected by dispersion, is required to shed light on Mediterranean fruit fly ecology and biology.

The general theory regarding discrete populations of a given species interconnected by migration, i.e., metapopulation, was developed by Levins (1969a, b, 1970). According to the classical metapopulation

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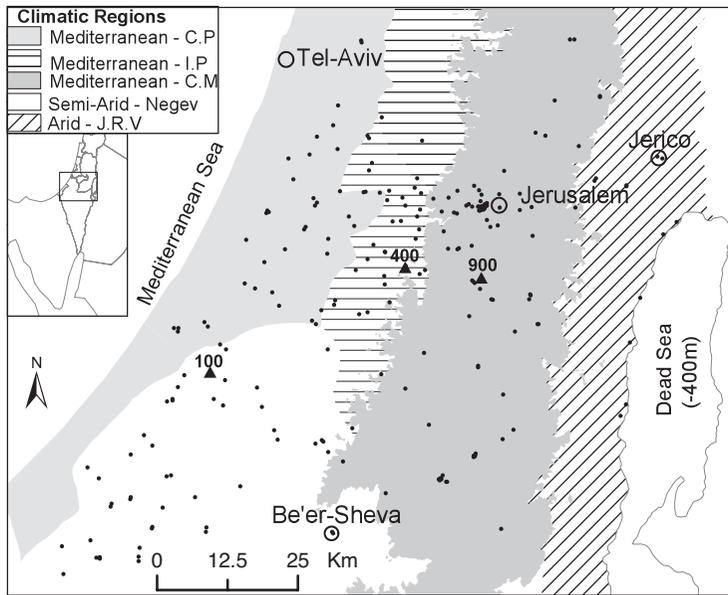
Fig. 1. Division of the study area according to climatic and host characteristics. Dots represent traps location. The small map on the left shows the location of the study area within the Near East. Triangles indicate the location of the sites in Table 1. C.P., costal plain; I.P., inner plain; C.M., central mountains; J.R.V., Jordan rift valley.

structure, all populations are subject to extinction and therefore the long-term persistence of a species can only occur at the metapopulation or regional level. Boorman and Levitt (1973) have introduced a modified model of metapopulation dynamics, where a constantly persistent population (i.e., the mainland) consistently supplies individuals to distant isolated populations (i.e., the islands), which may, from time to time, become extinct due to either deterministic or stochastic effects. The mainland-island metapopulation point of view is relevant to Mediterranean fruit fly population dynamics in our study system. In this case, the overwintering population represents the mainland population, having low probability of extinction and supplying individuals to the cold area populations on a seasonal basis. Such large-scale (meta)population dynamics may have far-reaching consequences both for basic and applied research of Mediterranean fruit fly.

The aim of this study is twofold. First, we present Mediterranean fruit fly spatiotemporal population dynamics at a mainland-island scale to demonstrate its consistent directional dispersion dynamics as a sequence of appearance through space and time. This is done by intensive monitoring of Mediterranean fruit fly populations followed by an analysis of weekly distribution maps obtained with a geographic information system (GIS). Second, we discuss the consequences of Mediterranean fruit fly large-scale, spatiotemporal dynamics, and the recently obtained data regarding its absence from the central mountains during the winter (Israely et al. 2004), for basic and applied research. In particular, we suggest that the currently used control practices of Mediterranean fruit fly should be reconsidered and changed accord-

ing to the existence of large-scale (meta)population dynamics.

Materials and Methods

Study Site. We conducted our study for 2 yr (15 October 1999–29 December 2001) over an area of 6,875 km². The area was confined by the Mediterranean Sea to the west, the Dead Sea to the east, the Tel-Aviv area to the north, and Beer-Sheva to the south (Fig. 1). The central mountain range (800–900 m in altitude) spans from north to south, resulting in segregation of the coastal plain (sea level) in the west from the Jordan Valley (−400 m in altitude) in the east. Winter (December–March) in Israel is cold and rainy, and summer (June–September) is hot and dry. Higher temperatures and higher precipitation characterized the winter of 2001 compared with winter 2000 (Table 1). We divided the study area into five regions according to climatic and biogeographic characteristics (Fig. 1; Table 2). We used "chilling portion" units as a criterion to determine the relative severeness of the 1999–2000 and 2000–2001 winters. Chilling portions are the measuring units of effective chilling accumulation needed to break dor-

Table 1.   Climate data for the winters of 2000 and 2001 at three altitudes (see Fig. 1 for sites location)

Altitude (m)	2000			2001		
	Precipitation (mm)	<8°C (h)	Chilling portion	Precipitation (mm)	<8°C (h)	Chilling portion
100	273	240	47	457	135	31
400	286	680	59	387	569	44
900	465	1429	86	546	690	75

Table 2.   Geographic, climate, and hosts characteristics of the main regions within the study area

Category	Coastal Plain	Inner Plain	Central Mountains	Negev	Jordan Rift Valley
Altitude (m)	0–200	200–400	400–1000	100–300	−400–400
Precipitation (mm)	400–600	400–500	600–700	100–250	50–200
Avg. Temp. (˚C)					
Aug.	26–28	26–28	24–26	26–28	30–32
Jan.	12–14	10–12	8–10	10–14	12–16
Climate type	Mediterranean	Mediterranean	Mediterranean	Semiarid	Arid
Main commercial hosts	Citrus, subtropic, deciduous	Deciduous, subtropic	Deciduous	Citrus, vine[a]	Palm, citrus, vine[b]

Climatic data were taken from Sofer (1995).
[a] Mainly wine grapes (a poor *C. capitata* host).
[b] Mainly table grapes (a good *C. capitata* host).

mancy according to the Dynamic model (Erez et al. 1988). Each chilling portion is equivalent to 28–30 continuous hours of exposure to 6°C or equivalent (<13°C).

Hosts. Private home gardens with various fruit-bearing host plants, including *Citrus* spp., with ripe fruits can be found throughout Israel in all regions and at all seasons, including winter (Bodenheimer 1951). Commercial plots in the mountains consist of early summer hosts maturing from May to June (e.g., cherries, *Prunus avium* L.; and apricots, *Prunus armeniaca* L.), and summer hosts maturing from June to October (e.g., pears, *Pyrus communis* L.; apples, *Pyrus malus* L.; nectarines, *Persica vulgaris* Miller, and peaches, *Prunus persica* L.). In the lowlands, citrus trees are the most common hosts grown at elevations <200 m. At altitudes of 200–400 m, summer deciduous (e.g., apricots, peaches, and nectarines) and subtropical orchards (e.g., persimmons, *Diospyros kaki* L.; and avocados, *Persea americana* Mill.) are the most common. Commercial hosts of the Jordan Rift Valley include citrus; grape vines, *Vitis vinifera* L.; and dates, *Phoenix dactyliferas* L. (Table 2).

Monitoring and Analysis. To determine what type of trap to use we compared (N.I., unpublished data) three trap types containing trimedlure, a male attractant. These included 1) Nadel (Nakagawa et al. 1971), the common trap type used in Israel for studies and commercial monitoring; 2) Jackson (Epsky et al. 1996); and 3) Tephri (Katsoyannos et al. 1999). In addition, we tested 4) a McPhail trap type containing a female specific attractant (Biolure, Consep, Bend, OR) (Israely et al. 2004). We found all trap types to produce the same qualitative results, in terms of seasonality and numbers. The Jackson trap main disadvantage is that its sticky surface is small and limited to several hundred flies per trap (Katsoyannos 1994) and thus is unsuitable for many sites and for long periods. Hence, we used the Nadel type trap, which is convenient, easy to service, and inexpensive (Katsoyannos 1994). Furthermore, Israely et al. (2004) have shown Nadel traps to be very effective in detecting small populations. They also found good correlation between male early trapping and early fruit infestation, indicating the simultaneous spatiotemporal distribution of both sex.

During 2000 and 2001, we deployed 255 and 159 traps, respectively (see Fig. 1 for trap locations throughout the study area). Due to technical and logistical limitations, some traps were not monitored every week. Traps were placed throughout the study area both in commercial orchards and home gardens. We preferred to place traps in home gardens containing a mix of winter, spring, and summer hosts to increase the sensitivity of the monitoring system. Host plant type and geographic location, including altitude, were recorded for each trap. Then the descriptive data and weekly fly catches were incorporated into a GIS database (ArcGIS 2001). Weekly spatial distribution charts were produced by plotting a GIS layer of the fly-trappings and over it a second GIS altitudes layer from which the highest altitude where flies were caught that week could be determined. We determined the "no-flies zone" area by analyzing all active traps in a particular week, defining those traps that caught flies at the highest altitude. As a result, we drew a two colored map: one color for the area where Mediterranean fruit fly was absent from (higher altitude region), and the other color was for the area where flies were found (lower altitude region). Consequently, if we detected a single fly in a single site at a given altitude, we assumed that flies might also be present at other sites at the same, or at lower altitudes. We then visually compared successive maps and looked for the spatial changes as well as for changes in population density in different sites.

Results

The annual population dynamics of Mediterranean fruit fly in the lowlands differed from those in the highlands. Below, we review Mediterranean fruit fly dynamics in each region separately and then collectively to describe the full spatiotemporal dynamics.

Lower Altitudes (<400 m). Flies were trapped year-round both during 2000 and 2001 with a total of 344,273 and 303,758 individuals, respectively (Figs. 2 and 3). Due to lower temperatures during 2000 (Table 1), summer fly population occurred later that year compared with 2001 (Figs. 2 and 3). Figures 2 and 3 also indicate that only few flies were trapped in the winter (January–March) (mean ± SD, 0.2 ± 1.3 and 1.9 ± 10.9 flies per week per trap for 2000 and 2001, respectively), mostly in home gardens and citrus groves <100 m in altitude. During the spring (April–
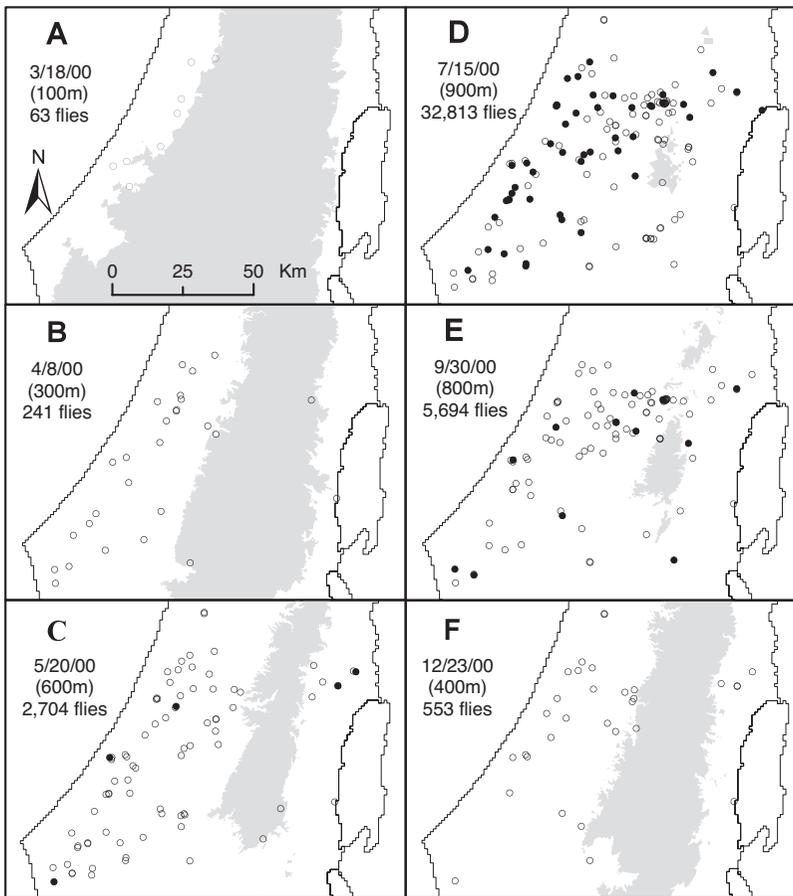
Fig. 2. Spatial distribution of Mediterranean fruit fly during 2000. Each subplot gives the total number of flies captured during the indicated week, their spatial distribution, and the maximum altitude above which no flies were caught (gray area). Empty dots represent traps with 1–100 flies per week; full dots represent traps with >100 flies per week. Traps with no flies are not presented.

June), flies increased rapidly in numbers and gradually were trapped in more sites and at higher altitudes (mean ± SD, 40.7 ± 225 and 89.5 ± 430 flies per week per trap for 2000 and 2001, respectively) (Figs. 2–4). Fly numbers remained relatively high between April and August (hereafter "reinvasion phase"), showing a pronounced peak in summer population between May and June and the end of August. A second smaller peak followed between September and November (Fig. 4; see also Avidov 1961). During the winter (January–March), fly numbers decreased rapidly, and as winter commenced flies were limited to low-altitude *Citrus* spp. and home gardens (Fig. 4). Note that although Fig. 4 indicates that fly density almost reaches zero during the winter (see also the values given above for the period of January–March), the population is viable (Bodenheimer 1951, Avidov 1961).

Higher Altitudes (>400 m). During 2000 and 2001, only 15 and 33 flies were trapped, respectively, from 1 January to 15 April (Figs. 2 and 3). Incidents of fly capture during this period were sporadic and rare and were limited to altitudes <600 m. In total, 74,425 and

72,723 flies were caught at >400 m altitude during 2000 and 2001, respectively. The established populations at altitudes <400 m caused a gradual expansion of flies to the higher altitudes during April and through June. In general, the higher the site, the later flies occurred at that site (Figs. 2 and 3). At 400–500 m, flies were captured from May. In July, a distinct peak was detected in most sites at all altitudes (Fig. 4). In sites with summer hosts, a second peak was detected during September–October (Israely et al. 2004). During the fall, flies steadily disappeared from the mountains, starting at the highest altitude followed gradually from lower sites, until no flies at all were trapped in January.

During the spring, as aerial sprays over citrus groves in the lowlands ceased (Roessler and Chen 1994) and temperature rose, fly populations increased. Consequently, flies gradually occurred at higher altitudes (Figs. 2 and 3). Invading flies penetrated the mountains both from the west (i.e., coastal plains) and from the east (i.e., Jordan Valley), establishing ephemeral populations along the route of invasion. In general, population fluctuation pattern in the mountains, >400 m, followed the same pattern of the lowlands,
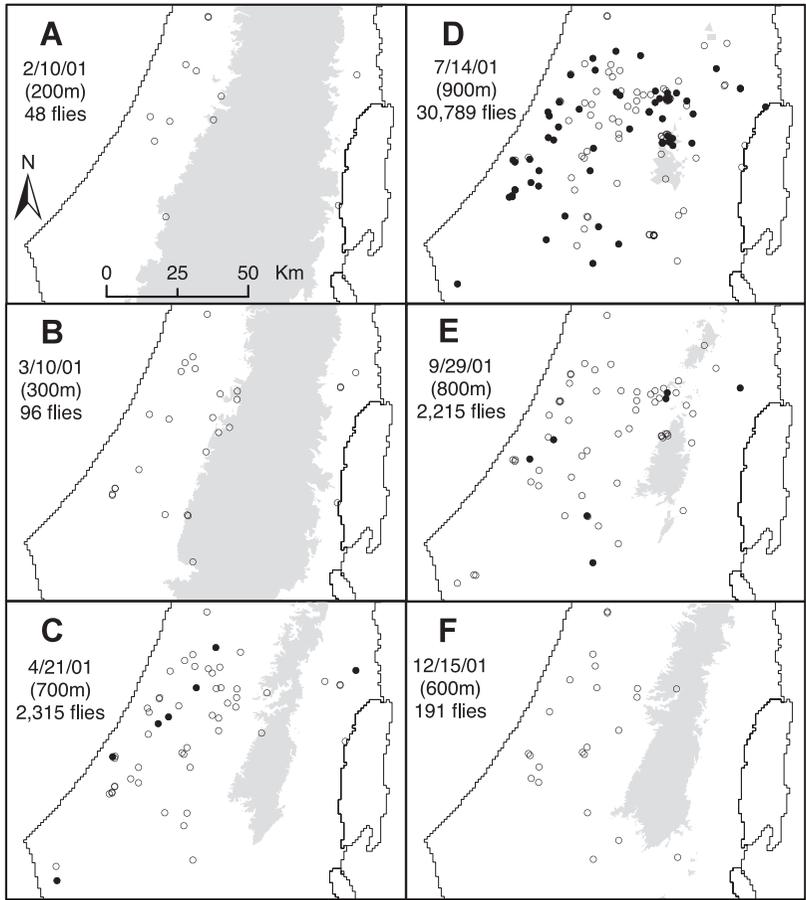
Fig. 3. Spatial distribution of Mediterranean fruit fly during 2001. Each subplot gives the total number of flies captured during the indicated week, their spatial distribution, and the maximal altitude above which no flies were caught (gray area). Empty dots represent traps with 1–100 flies per week; full dots represent traps with >100 flies per week. Traps with no flies are not presented.

although lagging behind and usually exhibiting lower population sizes. The mountain population declined sharply in August, several weeks before the lowland population decline. Continuous population decrease took place throughout the entire study area during fall and winter, up until January when flies were no longer captured in the mountains (Fig. 4). In contrast, in the lower altitudes (<400 m) flies were constantly caught, with the minor exception of winter 2000–2001, at altitudes of 200–400 m. The complete absence of flies from sites >600 m for 4 to 6 months in a row, during the fall and winter, is probably the most significant difference from the lowland population pattern. The same was true, but with somewhat shorter periods of
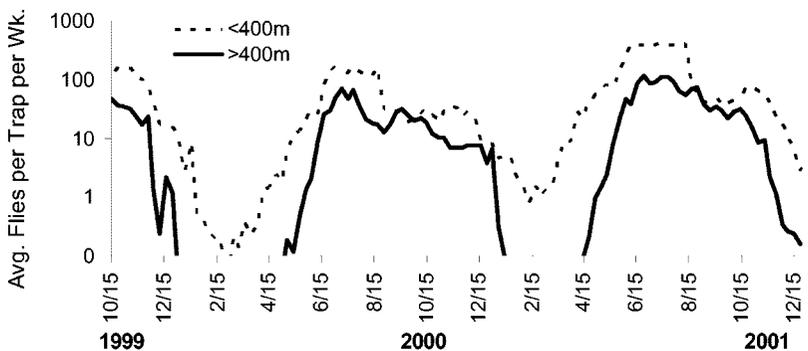

Fig. 4. Annual population fluctuations (log scale) in two altitude ranges, from 15 October 1999 to 31 December 2001.
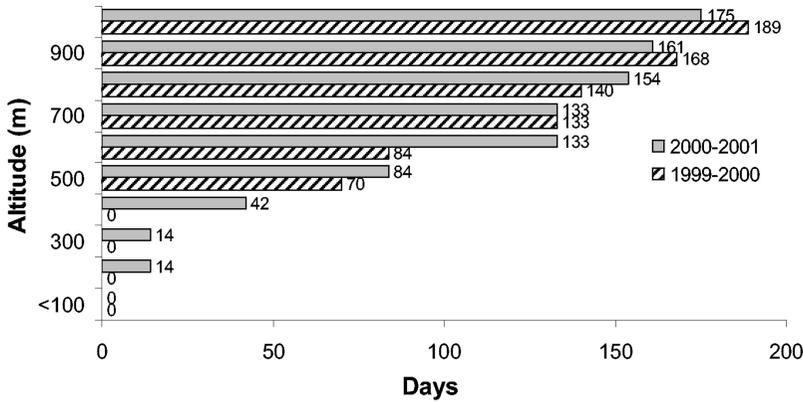
Fig. 5. Longest consecutive period (in days) during which no trappings were recorded in any of the traps, for altitudes from −400 to 1000 m. Traps were monitored from the beginning of October until the end of the following July for each year.

fly absence, for 500–600-m altitude compared with the lowlands.

Comparison between Altitudes. The higher the altitude, the longer the period of time during which flies tended to be absent (Fig. 5). In 2000, L (the longest consecutive period during which flies were absent from a trap) was, on average, ≈1 mo longer for traps at higher altitudes than at lower altitudes (mean ± SE, 18.6 ± 0.6 and 14.6 ± 0.5 wk for higher and lower altitudes, respectively). In 2001 the difference was even greater, close to 3 mo (mean ± SE, 21.7 ± 0.9 and 10.2 ± 0.9 for higher and lower altitudes, respectively). It may be that the variability between 1 and 3 mo was due to different weather conditions in the 2 yr. (We remark that, due to the large number of traps and their geographical dispersion, it was impossible to monitor each trap every week during the entire 2-yr study. There were thus traps for which L could not be accurately determined: for example, if a trap was inspected weekly and found empty for 16 wk, not inspected for 4 wk and then inspected and found to contain flies, it was impossible to determine when during the 4 wk the flies arrived. In such a case, we imputed a value for L by assuming that the flies arrived at a random time during the nonmonitored period.)

To focus on the influence of altitude on Mediterranean fruit fly presence during the winter, Table 3 presents results for traps which were continuously monitored for 12 consecutive weeks from mid-January through March 2000 and 2001. Traps were declared "empty" if they had no catches during the entire 12-wk period. For both years, the number of empty traps was considerably larger at higher altitudes than at lower

altitudes. In fact, in 2000 all of the 24 traps >400 m in altitude were empty during the entire period.

Discussion

Our results show that flies are absent from the high altitudes (>400 m) in the central mountains of Israel during the winter, whereas they are consistently present along the coastal plain and the Jordan Valley. These findings agree well with previous reports (Bodenheimer 1951; Avidov and Harpaz, 1969; Israely et al. 1997, 2004) and with the observations of Israely et al. (2004) that Mediterranean fruit fly cannot survive the winter in the mountains of Israel. However, here we present for the first time the change in Mediterranean fruit fly distribution in space and time over a large geographic area (Figs. 2–3).

The general pattern emerging from the spatial distribution maps suggests the following three phases: 1) overwintering—Mediterranean fruit fly survives in suitable sites (i.e., the coastal plain and The Jordan Rift Valley), which are relatively warm and contain a large amount of winter hosts (see Messenger and Flitters 1954 for bioclimatic characteristics of overwintering areas); 2) reinvasion—after population increase, offspring of the overwintering population leave the sites and gradually reinvade sites from which the fly had disappeared during the winter. The large quantity of fruits left on citrus trees after picking (May–June), together with the relatively high temperatures and the termination of control sprays, create a suitable environment for a rapid population increase; and 3) dwindling—fly population size decreases in all sites. Full disappearance occurs at high altitudes, whereas small-sized populations remain overwintering in the warmer areas.

The large-scale pattern emerging from the above-mentioned spatiotemporal dynamics resembles a mainland-island metapopulation structure (Boorman and Levitt 1973, Hanski 1999) in which the coastal plain is immune from extinction, whereas the high-altitude mountain areas experience seasonal extinctions and

Table 3. Number of traps empty during the winter (mid-January–March)

Year	2000		2001	
Altitude	<400 m	>400 m	<400 m	>400 m
No. empty traps	15	24	11	43
Total no. traps	29	24	51	47
Proportion	0.52	1.00	0.22	0.92

are recolonized at a high directional dispersion rate. Consequently, this metapopulation structure emphasizes the connection and dependence of the high-altitude mountain populations on the coastal plain populations. We argue that this pattern may have further consequences for our understanding of various biological aspects, such as the genetic variability of the current populations as well as large-scale oriented control and eradication strategies. For example, genetically, it is possible that because the ephemerally high-altitude populations breed for several generations in the mountains and thereafter individuals may migrate back and breed in lower altitude areas, they may contribute significantly to the maintenance of several phenotypes and genotypic variations that might have become extinct without the overall spatiotemporal dynamics. To our knowledge genetic studies of Mediterranean fruit fly that investigate the contribution of a mainland-island structure on genetic variability have not yet been performed.

Control and eradication strategies are currently based on the assumption that populations are basically "local" and flies usually disperse only hundreds of meters throughout their life. Thus, control treatments are given individually to every orchard or group of orchards without considering the possible effect of invasion of distant populations. However, our results suggest that such a strategy may be ineffective given the dispersal ability of Mediterranean fruit fly and the directional interrelation between its subpopulations. Consequently, any effective control and/or eradication strategy should focus on treatment campaigns covering large areas, which consider the change in Mediterranean fruit fly distribution in space and time. A large-scale campaign does not necessarily mean that the entire area needs to be treated, but rather, that we may be able to focus on specific overwintering populations, located within particular climatic and geographic areas. Furthermore, our GIS-based approach and the high consistency between our 2 yr of study suggest that future multivariate statistical analyses may direct to some source populations on which control treatment may be more effective than on other populations. Additionally, the metapopulation approach may allow us to focus on main dispersal routes by which flies may penetrate the invaded areas.

In sum, the recently gathered data demonstrate that a metapopulation-like structure, maintained through directional dispersal, characterizes the distribution and appearance of Mediterranean fruit fly populations in different nonindependent locations. Throughout this article we provide, for the first time, evidence for the spatiotemporal dynamics of Mediterranean fruit fly distribution in a heterogeneous large-scale landscape. Given the heterogeneity of many landscapes in which Mediterranean fruit fly populations occur, it is likely that such spatiotemporal dynamics characterize other landscapes as well. We strongly suggest that understanding such dynamics should have far-reaching consequences for our future basic research as well as practical applications.

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Metapopulation Spatial–Temporal Distribution Patterns of Mediterranean Fruit Fly (Diptera: Tephritidae) in a Patchy Environment

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ABSTRACT We studied the large-scale spatial–temporal distribution pattern of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) to understand whether long-term dispersal may affect its maintenance in a highly patchy and isolated arid environment. The study area contained few dispersed settlements and agricultural plots covering 3,000 km^2, ranging from 100 to 900 m in altitude in southern Israel. Due to the arid nature of the study area, no wild hosts existed outside the settlements. Data were collected from three settlements at different altitudes from 1999 to 2002. During 2000, adult flies were monitored throughout the entire area. Data were incorporated into a geographic information system, and weekly spatial distribution charts were produced and analyzed. Our results suggest that, within the study area, *C. capitata* overwinters in sites <400 m in altitude with abundant winter hosts but not at higher altitudes. In remote settlements and agricultural areas at higher altitudes, flies reappeared every year in midsummer, which can only be explained by annual migration from the lower altitudes. Our results demonstrate that flies migrate at least 50 km, probably over a single generation, before reaching some of the remote havens within the study area. This long-distance migration has far-reaching consequences for maintenance of remote populations and should be taken into consideration for future basic research and applied control practices of *C. capitata*.

KEY WORDS *Ceratitis capitata*, large-scale population dynamics, long-distance dispersal, local extinction, recolonization

THE MEDITERRANEAN FRUIT FLY, *Ceratitis capitata* (Wiedemann), draws much attention from entomologists, ecologists, and pest control specialists throughout the world. It is found on all continents, except Antarctica, and is the cause for annual damage of millions of dollars around the world (Siebert and Cooper 1995, Mumford et al. 1995, Enkerlin and Mumford 1997). As a result, it is the target of numerous eradication campaigns and vast control actions wherever it exists, as well as costly preventive programs in places where it might strike, e.g., California. In Israel, in spite of routine control and temporary population reduction, fly populations seem to recover rapidly (Israely et al. 1997). This phenomenon suggests that the contemporary control strategies tend to ignore the spatial–temporal dispersal of the *C. capitata.*

Most *C. capitata* control strategies rely on the assumption that *C. capitata* individuals, due to their small body size, have relatively limited dispersal (Wakid and Shoukry 1976, Hagen et al. 1981, Plant and Cunningham 1991). Therefore, moving through "hostile" environments to distant patches is predicted to be limited, and natural dispersal is often considered possible for no more than a few kilometers. As a result, large-scale dispersal and dynamics of *C. capitata* have been largely neglected through the years. However, if *C. capitata* is capable of long-distance migration, one must determine how it affects processes at the regional spatial scale, as suggested by ecological theory. For example, metapopulation dynamics (Hanski and Gilpin 1997, Hanski 1999) explicitly suggests that long-term persistence is affected by between-locality processes, such as dispersal and extinction (Levins 1969a). Therefore, it has to be considered when designing a pest control and eradication strategy (Levins 1969b).

Israely et al. (2004) and Israely and Oman (2005) showed that the *C. capitata* does not survive the winter in the central mountains of Israel but reinvades them in the early summer from the Mediterranean coastal plain in the west and the Jordan rift valley in the east (Israely et al. 2005). The reinvasion from the Jordan Rift Valley requires the migration of individuals over
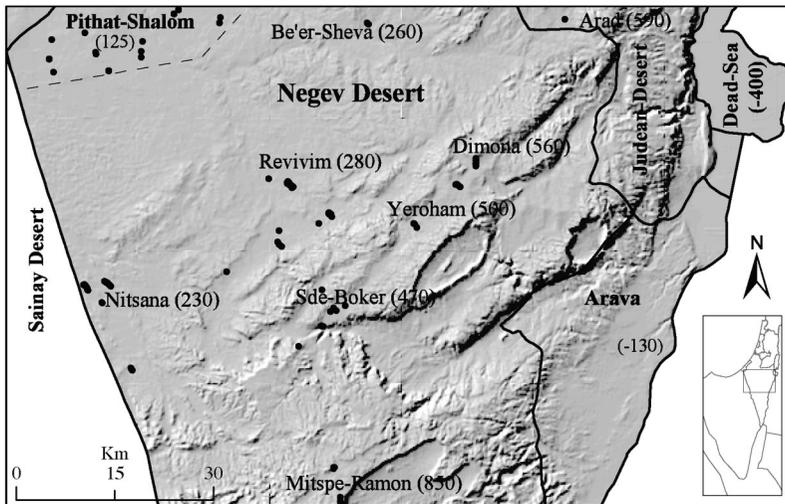
Fig. 1. The study area is located at the southern Israel (small map on the right). It is surrounded by the Dead Sea and the Arava desert on the east, Sinai desert on the west, the southern Negev on the south and the temperate part of Israel at the north. Most hosts within the study area are concentrated in Pithat-Shalom district and its surroundings, on the northwestern Negev. Altitude is given in parentheses.

the hostile environment of the Judean desert. However, this east–west dispersal axis is relatively short, with many intermediate suitable feeding and oviposition habitats within the 10–30 km between the source of the migrating flies and the central mountains. Under such conditions, even a relatively small number of flies could establish a significant population through short-distance reinvasion. Once flies reach the central mountains, they encounter a densely populated region with many home gardens having diverse hosts suitable for feeding and oviposition, in addition to extensive commercial agriculture (Israely et al. 2004, Israely and Oman 2005).

Unlike the central region, the southern part of Israel is characterized by a large desert, having sparse settlements or agriculture within large, hostile, host-free environments. Dispersal between potential breeding areas requires that *C. capitata* would cover distances of 30–60 km without intermediate stopovers. In this study, we investigated the spatial–temporal dynamics of *C. capitata* in southern Israel with arid environmental conditions. Because Israely et al. (2004) and Israely and Oman (2005) already demonstrated that flies do not survive the winter in such altitudes, in the central mountains of Israel, it is unlikely that they can survive the cold winter of the Negev highlands. This assumption also is supported by preliminary data from the Negev highlands of not observing flies or infested hosts during the winter and spring. We therefore ask whether *C. capitata* is capable of long-distance dispersal and whether *C. capitata* populations in distant localities can persist through extinction–reestablishment processes. We propose that we can gain strong support for the hypothesis that *C. capitata* individuals can move long distances if similar spatial–temporal dispersal patterns repeat themselves annually in different locations. Such repetitive patterns are unlikely

to depend on stochastic mechanisms, such as accidental transfer by humans. We argue that because the patchy desert distribution of the fly is not unique to the southern desert of Israel but occurs in many deserts around the world, it is important to understand *C. capitata* ecology under such conditions and clarify the mechanisms enabling it to exploit those regions.

Materials and Methods

Study Area. We conducted our study over an area of 3,370 km² in southern Israel within the Negev desert (Fig. 1). Although the northern part of the study area is semiarid, its central and southern parts are arid, receiving <150 mm of rainfall per year. The average temperature during January is 8.5°C at the highest elevations and 11.5°C at the lower elevations, and in August it is 24 and 25.5°C, respectively (Kurtzman and Kadmon 1999). Precipitation occurs during winter (January–March) and ranges from 70 mm at 900-m altitude to 100–250 mm at 100–300-m altitude, respectively.

Hosts and Monitoring. Most hosts are concentrated within the northwestern part of the study area, which includes extensive citrus orchards, i.e., the Pithat-Shalom district. South of this area, in a region of >2,700 km², the main suitable hosts in this area include a small plot of citrus and some deciduous trees are in Revivim, another deciduous plot is located in Sde-Boker, and a prickly pear (*Opuntia* sp.) farm is located next to Dimona (Zabarey Orly). However, in all settlements a variety of summer and winter hosts can be found in private home gardens. Although the cultivated hosts are irrigated, no hosts and almost no vegetation are found in the wild.

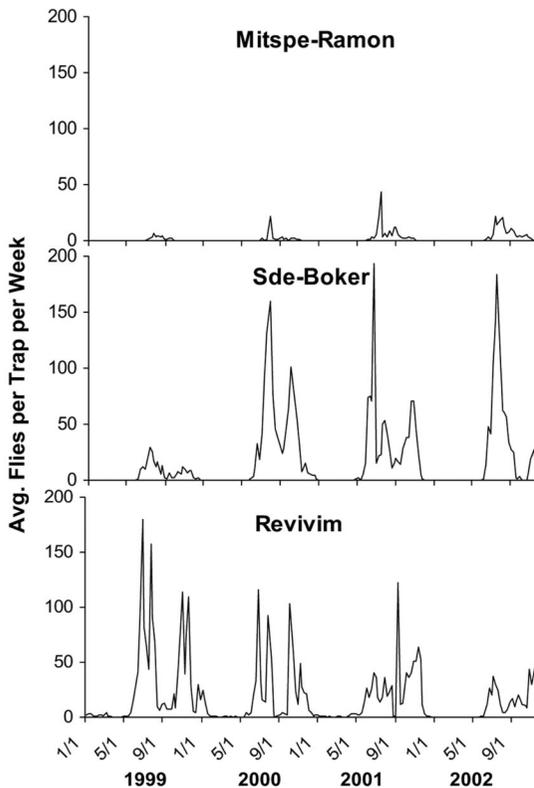The adult metapopulation pattern was studied by weekly presence–absence distribution maps. These

Fig. 2. Population fluctuations in three settlements located at different altitudes and distances from the highly cultivated area at northwestern Negev from 15 January 1999 to 31 December 2002.

maps provide movement sequences, which can be related to altitude and temperature and to host. Male flies were captured by three types of traps, all using trimedlure (Hentze 1993) as an attractant: Nadel (Nakagawa et al. 1971), Jackson (Epsky et al. 1996), and Tephri (Katsoyannos et al. 1999). We found all trap types to produce the same qualitative results in terms of seasonality and numbers. A total number of 223 traps was deployed and serviced throughout the north and central Negev desert from January to December 2000 (hereafter, the extensive survey). Only a few settlements exist at altitudes >400 m; thus, a limited number of traps was placed there. Due to logistic limitations, technical constraints, and high wear on the traps, the actual number of weekly traps varied between 99 and 165 but was usually >130. Traps were located in commercial orchards as well as in home gardens and were maintained, monitored, and recorded weekly. A separate set of data was collected from 1999 to 2002 from three representative settlements in the study area: Revivim (290 m), Sde-Boker (470 m), and Mitspe-Ramon (850 m), hereafter the long-term survey. In addition to altitude differences, these settlements differ in distance from the main citrus-growing area in northwestern Negev—29, 49, and 74 km, respectively. The number of traps varied within and between years during the study period.

From 1999 to 2002, the following number of traps was monitored and serviced weekly in Revivim (21, 24, 24, and 21), Sde-Boker (12, 8, 4, and 4), and Mitspe-Ramon (6, 13, 10, and 10).

Data Analysis. The following data were recorded for each trap: host plant type and geographic location, including altitude. For each trap, descriptive data and weekly fly catches were incorporated into a geographic information system (GIS) database (ArcGIS 2001). Trapping levels were related to the geography, climate, and hosts of the different locations. Weekly spatial distribution charts were produced by plotting a layer of trapped fly number and over it a second layer indicating the highest altitude where flies were caught that week. We determined the "no-flies zone" area by analyzing all active traps in a particular week, defining those traps that caught flies at the highest altitude. As a result, we drew a two-color map: one color for the area where *C. capitata* was absent (higher altitude region), and the other color for the area where flies were found (lower altitude). Consequently, it was enough to detect a single fly, in a single site, at a given altitude, to declare that flies might be present also in other sites in the study area that shared the same or lower altitude. We then visually compared successive maps and looked for spatial changes as well as for changes in population density in different sites. Because Israely et al. (2004) demonstrated that very low population levels could be effectively detected by the same trapping method we have used, we assumed that the probability of presence of flies is extremely low when trapping level is zero.

Results

The long-term trapping data (1999–2002) collected from Revivim, Sde-Boker, and Mitspe-Ramon indicate that both between- and within-year population dynamics in the study area were consistent and highly predictable. Although the number of trapped flies changed through the years, the basic temporal patterns of population appearance and disappearance, timing, and often size of peaks remained almost unchanged (Fig. 2). In Revivim, the most northern and warmer of the three locations, a low population size was maintained throughout the winter, followed by a sharp increase in population size during the spring and summer (first peak) and then another increase during the fall (second peak). In contrast, both in Sde-Boker and Mitspe-Ramon no flies were trapped from winter to early summer (December–May). Flies were first caught in Sde-Boker in late May and by early June in Mitspe-Ramon. The first noticeable summer peak in Revivim was in early July, followed by a smaller peak in Sde-Boker, and a smaller peak by mid- to late July in Mitspe-Ramon (Fig. 2). Following the same pattern, during the fall, flies first disappeared from Mitspe-Ramon and then from Sde-Boker, but, as mentioned above, they remained at very low abundance during the winter in Revivim. Specifically, a very consistent and annual repetitive pattern in peak formation— number of peaks and temporal appearance—in the
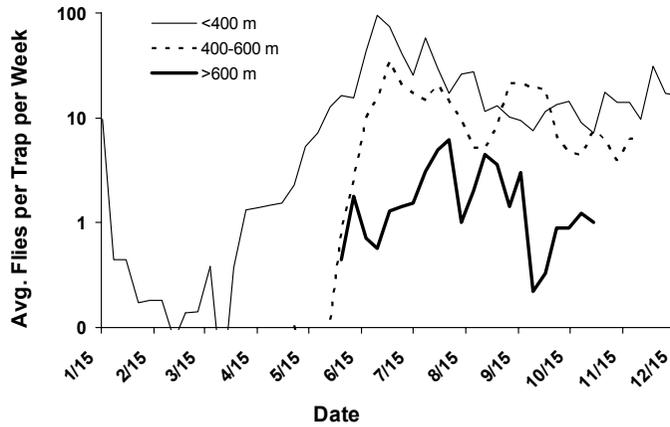
Fig. 3. Temporal population fluctuations (log scale) in three altitude ranges during 2000. Traps sample sizes from lowest to highest altitude are 157, 80, and 15, respectively.

three locations during the four consecutive monitoring years (Fig. 2).

In the extensive survey, we trapped in total 74,091 flies during 2000. Figures 3–5 indicate that *C. capitata* dynamics was strongly related to altitude differences and hence to climatic conditions, i.e., a warm-to-cold gradient. Although in small numbers, *C. capitata* individuals were captured throughout the winter at locations <400 m in altitude (Figs. 3 and 4). From 15 January to 1 April 2000 (i.e., winter), 1,124 flies were captured at <400-m altitude (mean ± SD, 0.4 ± 1.95). During the same period, only seven flies were captured at >400 m (0.01 ± 0.116), all in five traps within a large prickly pear farm (i.e., Zabarey Orly) next to Dimona (Fig. 1), at 550-m altitude. The highest fly abundance was found in the northwestern study area, in a very large citrus-growing area, the Pithat-Shalom district (2.9 ± 3.1). Data collected in this area demonstrate a continuous presence of flies through the winter.

Similar to the long-term monitoring data, the magnitude of the population size peaks and their temporal appearances depended on altitude (Fig. 3). During summer, a pronounced peak occurred in late June at altitudes <400 m and then another peak was present during late November. At 400–600-m altitude, the summer peak occurred in early July with a rapid decline thereafter, followed by a smaller peak during September. Above 600 m, flies were first trapped during early June, with a small peak in late July and then gradually declined until disappearing by mid-November.

Discussion

Both data sets reveal a similar trend regarding the spatial–temporal pattern of *C. capitata* population dynamics in southern Israel. A consistent temporal pattern has been observed during the 4 yr of consecutive monitoring in all locations. This consistency relates to the similarity in the time of appearance and disappearance of *C. capitata* individuals during summer and winter, as well as to the timing of population peaks

within and between years. Furthermore, differences among locations remained relatively constant regardless of the distance between them. The major difference between the three locations of the long-term survey was that Revivim, the warmest and northernmost location, had a local population year-around, whereas Sde-Boker and Mitspe-Ramon did not support a winter population but most likely relied on a new fly introduction each year in early summer. As suggested by Israely et al. (2004) and Israely and Oman (2005) for the central mountains of Israel, overwintering in the Negev desert mountains is unlikely to be due to cold weather, lack of hosts, or the mutual effect of both factors, suggesting that the same factors were responsible for winter disappearance of *C. capitata* from the central mountains of Israel. Abundance peaks can be related to the spatial pattern observed for the altitudinal gradient along the north–south axis; in the summer, *C. capitata* individuals occur first in the lower altitudes and only later in the higher altitudes. In the fall and early winter, the pattern is reversed; flies disappear first from the highest altitudes and gradually from lower ones (Figs. 2 and 5). Consequently, temporal and spatial scales are related through the change of altitude-based climatic conditions through time. These results are well in line with our previous results showing that *C. capitata* overwinters in relatively warm areas, which are abundant with winter hosts, reinvade sites during the spring and summer from which they disappeared in the previous winter (Israely et al. 2004, Israely and Oman 2005).

In the current study area, fly populations can increase only within settlements and their vicinity, where hosts are available. Those areas are distant and remote from one another, surrounded by hostile desert environment. Under such circumstances, close stopovers or host-to-host dispersal sites are nonexistent. For example, the straight-line distance between Revivim and Sde-Boker is 20 km and the distance from Sde-Boker to Mitspe-Ramon is 30 km. Thus, given that *C. capitata* does not overwinter in these locations,
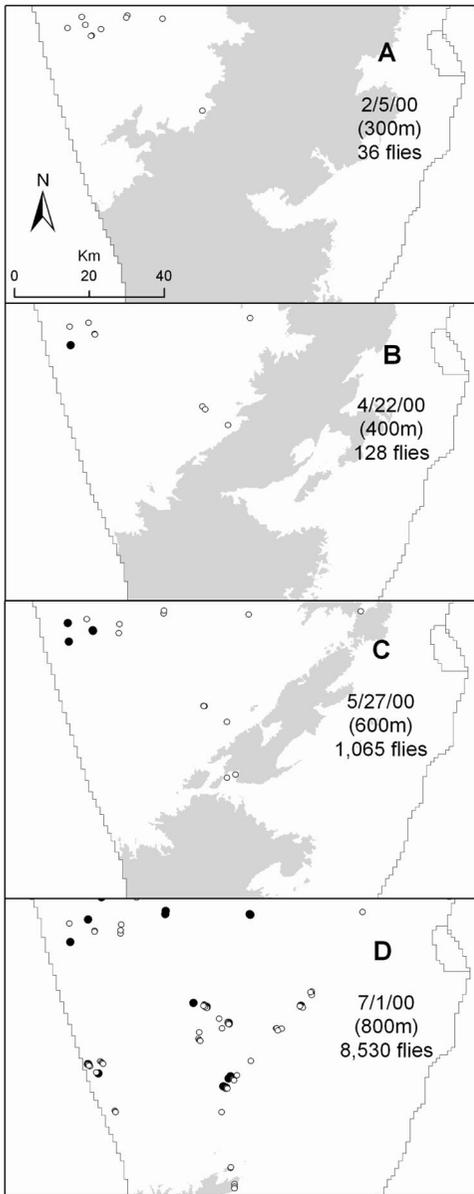
Fig. 4. Spatial distribution of *C. capitata* during spring and summer 2000. Each subplot represents a different time of the year (mo/d/yr) and gives the total number of flies captured during the indicated week, their spatial distribution, and the maximal altitude above which no flies were caught (gray area and number in parentheses). Empty dots represent traps with 1–50 flies per week; full dots represent traps with >51 flies per week. Traps with no flies are not presented. Due to the scale of the maps, several crowded traps may look like one.

Fig. 5. Spatial distribution of *C. capitata* during fall 2000. Each subplot represents a different time of the year (mo/d/yr) and gives the total number of flies captured during the indicated week, their spatial distribution, and the maximal altitude above which no flies were caught (gray area and number in parentheses). Empty dots represent traps with 1–50 flies per week; full dots represent traps with >51 flies per week. Traps with no flies are not presented. Due to the scale of the maps, several crowded traps may look like one.

long-distance dispersal is likely to take place. Furthermore, given the high consistency and similarity in population dynamics between years and between locations, it is unreasonable to explain the movement of *C. capitata* populations between locations simply by stochastic, human-based passive transport. If this were
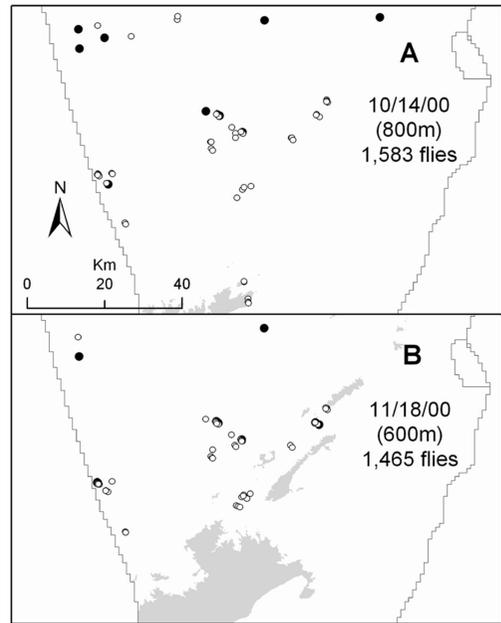
the case, we would expect a correlation between the size of human populations in settlements and the probability of detecting flies in early summer. However, such a correlation does not exist: the human population of Mitspe-Ramon is ≈50-fold larger than Sde-Boker or Revivim. Yet, flies were there last in the summer. Thus, *C. capitata* individuals must be regularly dispersing long distances to maintain the observed large-scale spatial–temporal distribution pattern.

The flight range and dispersal ability of *C. capitata* are fundamental to both ecological and control strategy issues. Currently, two opposing schools disagree regarding the lifetime dispersal range of *C. capitata*: the first suggests that it can fly no more than few hundred meters per day and a total of 1–3 km during its life span (Ezzat et al. 1970, Sharp and Chambers 1976, Wakid and Shoukry 1976, Hashem et al. 1980, Hagen et al. 1981, Plant and Cunningham 1991). The second school suggests that it can disperse tens of kilometers. Bateman (1972) reports about a study conducted by Steiner et al. (1962) in which *C. capitata* was found to move from 40 to 72 km, including 64 km over water. In another study, conducted in central Israel by Goldenberg et al. (1975), some 12,308 flies were recaptured 35–40 km away, out of 6.14 million sterilized, marked flies that were released. Furthermore, A. Yawetz (personal communication), who took part in

the above-mentioned report, informed us that some flies were found as far as 60–70 km from the release point. Goldenberg et al. (1975) suggest that the prevailing winds might have a substantial effect over the flies' migration direction. Harris and Lee (1987) suggested that the establishment of *C. capitata* in Hawaii may have been facilitated by its "long-range dispersal" abilities, which enable it to efficiently search and discriminate preferred hosts, and coexist with the oriental fruit fly, *Bactrocera dorsalis* Hendel. Whether *C. capitata* reinvasion is by active flight, passive carriage on the wind, or by a combination (Dobzhansky 1973) is another question that needs to be addressed in future studies. However, from *C. capitata* flight physiology (Sharp and Chambers 1976), it is most likely that *C. capitata* long-range flight is mostly passive: tethered flies were found capable of flying no more than 6.72 km in 203 min, flying 100% of the time (avg. 2 km/h.). Hence, using active flying alone would take the flies tens of hours before reaching the farthest sites, such as Mitspe-Ramon. With no "refueling" sites along the way, such a long active flight is impossible. Cases of long-distance dispersal have been described for many species of *Drosophila* invading oases in the Death Valley in California. The Death Valley *Drosophila* species, like *C. capitata*, are polyphagous, tropical in origin, and lack dormancy. For many years, *Drosophila* was believed to be a short-distance flier (<1 km) (Dobzhansky and Wright 1943, Dobzhansky 1973, Crumpacker 1973, Taylor et al. 1984), but later studies have strongly argued that this was not the case. Coyne et al. (1982, 1987) suggested that, although most *Drosophila* flies used trivial, short-distance movements, a small percentage of the population dispersed in the fall for long distances and hence reoccupied discrete habitats in the Death Valley (Coyne et al. 1982). Dobzhansky (1973) suggested that the short-distance movements of *Drosophila* spp. involve active dispersal, whereas its long-distance dispersal involves passive transport.

Our study shows that *C. capitata* individuals can disperse long distances in a consistent and predictable manner. Furthermore, given that flies occurred in Sde-Boker, a small, host-poor location, only a week before they were captured in Mitspe-Ramon, it is unlikely that the former is the source of the flies of Mitspe Ramon. Therefore, the source of Mitspe-Ramon's flies could be from the small population of Revivim area, ≈50 km away, or from the much larger population of Pithat-Shalom in the northwestern part of the study area, ≈74 km away. Additionally, if the tendency to migrate is density-dependent, then it is more likely that flies arrived from the northwestern region (i.e., Pithat-Shalom) of the study area, where host and population densities are several magnitudes higher than in Revivim. Interestingly, due to a massive sterile male release in most of the area covered by our study from January 2001 to August 2002, a population decrease was expected to occur if *C. capitata* populations rely only on local dynamics. However, Fig. 2 clearly shows that such a change has not been observed, because there was no change in the pattern of trapping during these years.

In general, as in our large-scale study in central Israel (Israely et al. 2004, Israely and Oman 2005), our current study suggests that *C. capitata* distribution resembles a mainland–island metapopulation structure (Boorman and Levitt 1973), where the mainland includes, among others, the costal plain and northern Negev. Such mainland populations consistently contribute dispersing individuals that form ephemeral populations along the route of dispersal (Hanski and Gilpin 1997, Hanski 1999). We suggest that *C. capitata* distribution cannot be explained without an understanding of its large-scale spatial–temporal dynamics. Furthermore, we suggest that all populations within the study area may belong to the same metapopulation (Hanski 1999) and therefore should be considered so for both basic and applied issues. Unfortunately, as we mentioned above, *C. capitata* control campaigns tend to ignore the large-scale distribution and population dynamics. Alternatively, they assume that *C. capitata* individuals have very limited dispersal ability and hence are not able to move through "hostile" environments to distant host-based patches. However, as we show here, such an assumption may be wrong and consequently may lead to a major failure to control or eradicate *C. capitata*, leading to an unnecessary waste of economic resources. We suggest that this may be the main reason for the unsuccessful eradication campaign currently running in the Arava desert (Rossler et al. 2000) and previously conducted in the Negev desert. As a result, we suggest that two main issues should be considered when an eradication campaign is proposed. First, the barrier width between treated and untreated areas should be ≈100 km, because *C. capitata* individuals may naturally disperse long distances on a routine basis. Second, if such a barrier is impossible, then broad consideration should be given, especially regarding neighboring populations, to the treated and the large spatial context of the future program, including specific parameters affecting dispersal (e.g., corridors and wind direction) and extinction (e.g., climatic conditions) processes. Interestingly, Levins (1969a) introduced the well known theory of metapopulation dynamics to suggest effective biological control to prevent the reestablishment of pests in treated patches from distant ones. We suggest that it is time to apply this theory to pest populations.

Acknowledgments

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