

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 km², 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 reinvansion from the Jordan Rift Valley requires the migration of individuals over

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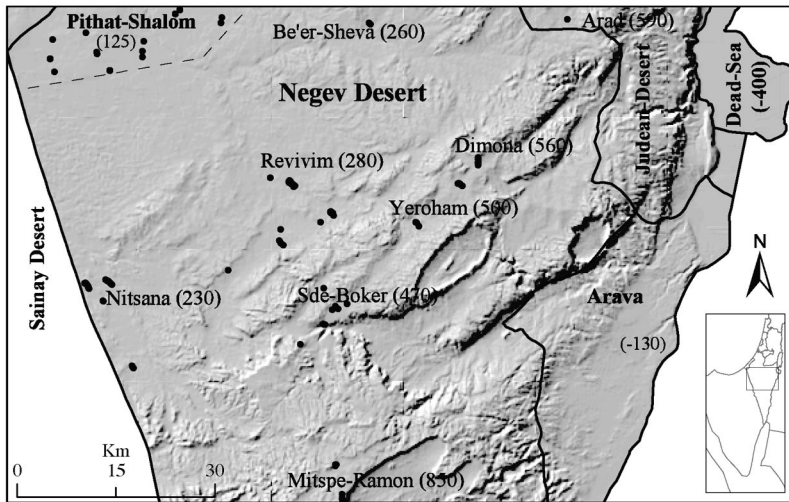


Fig. 1. The study area is located at the southern Israel (small map on the right). It is surrounded by the Dead Sea and the Arava desert on the east, Sinai desert on the west, the southern Negev on the south and the temperate part of Israel at the north. Most hosts within the study area are concentrated 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

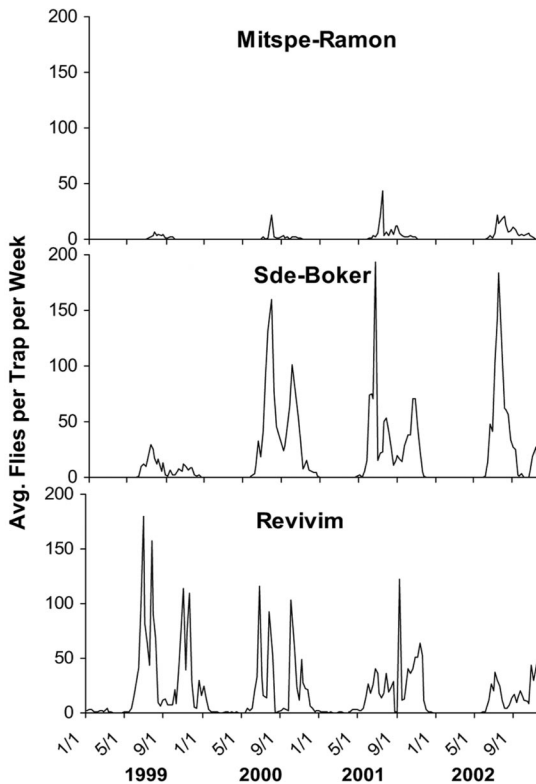


Fig. 2. Population fluctuations in three settlements located at different altitudes and distances from the highly cultivated area at northwestern Negev from 15 January 1999 to 31 December 2002.

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

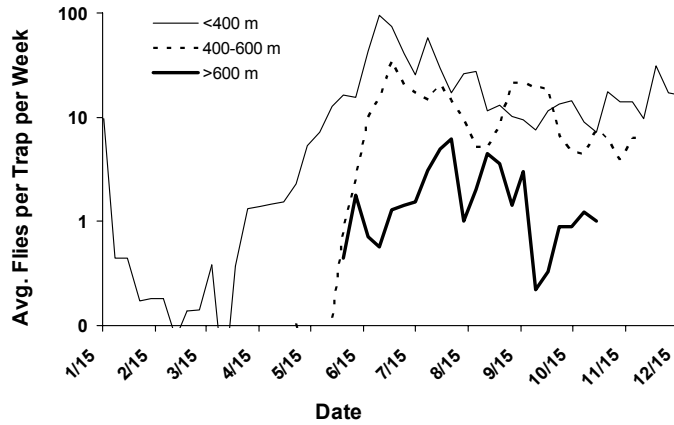


Fig. 3. Temporal population fluctuations (log scale) in three altitude ranges during 2000. Traps sample sizes from lowest to highest altitude are 157, 80, and 15, respectively.

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 \pm 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,

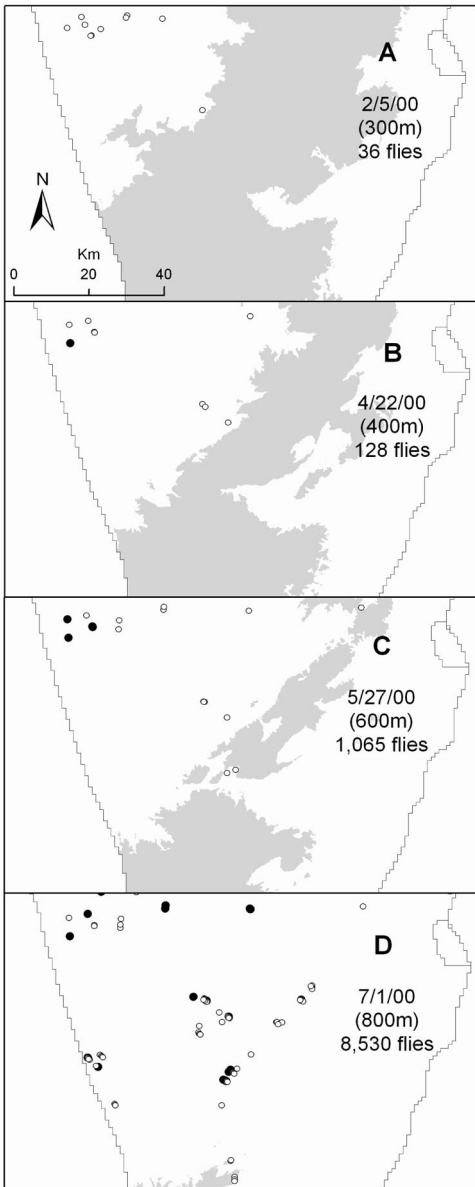


Fig. 4. Spatial distribution of *C. capitata* during spring and summer 2000. Each subplot represents a different time of the year (mo/d/yr) and gives the total number of flies captured during the indicated week, their spatial distribution, and the maximal altitude above which no flies were caught (gray 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.

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

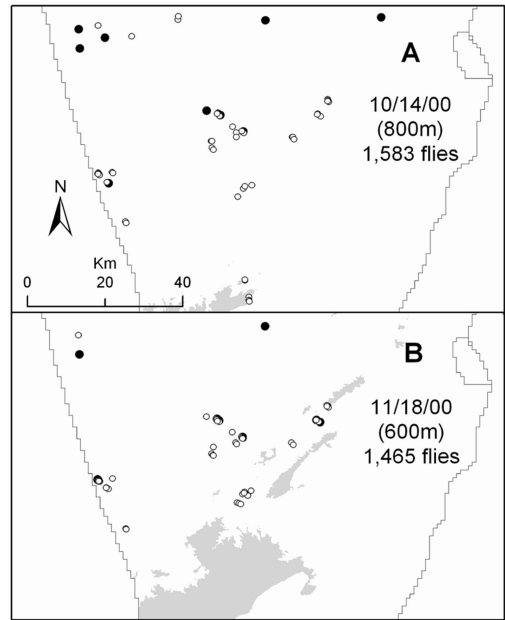


Fig. 5. Spatial distribution of *C. capitata* during fall 2000. Each subplot represents a different time of the year (mo/d/yr) and gives the total number of flies captured during the indicated week, their spatial distribution, and the maximal altitude above which no flies were caught (gray area and number 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.

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 coastal 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.

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