Establishment of the Mediterranean Fruit Fly in California

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Principles of invasion biology are brought to bear on the question of whether the medfly is established in California. Since its first discovery in 1975, the pest has been captured in the Los Angeles Basin in nine separate years including every year from 1986 through 1990. The trend has become distinct—the intervals between captures are decreasing, the numbers captured are increasing, and the area over which they are detected is expanding. In addition, appearances are seasonal and captures in recent years have occurred in many of the same cities and neighborhoods where medflies were found several years before. Evidence suggests that the medfly may be established in the Los Angeles area and that previous eradication programs did not eradicate the medfly from California. It follows that detection, exclusion, and eradication protocols may need to be reexamined.

MANY ENTOMOLOGISTS CONSIDER THE MEDITERRANEAN fruit fly, *Ceratitis capitata* (Wiedemann), to be one of the most destructive and costly agricultural pests in the world and, therefore, to pose an enormous threat to a state such as California with climatic and host conditions suitable for its establishment (*1*). In spite of intense efforts at exclusion, detection, and eradication of this fly, known as the medfly, the problem has become worse over the last several years in the greater metropolitan area of Los Angeles in the form of decreased intervals between appearances, increased numbers captured, and expanded area over which it is detected (*2*).

Understanding the nature of these reoccurrences—whether they stem from frequent reintroductions or an established population—is exceedingly important to both state and national interests for several reasons. First, medfly eradication and surveillance policy must flow from an understanding of the biological status of the target population. For example, tightening restrictions along potential entry pathways (mail and air- and seaports) will have virtually no effect on the medflies captured in the state if the flies stem from a resident breeding population. Second, determining the nature of the medfly reappearances will shed light on the success of previous eradication programs. Eradication strategy and criteria for declaring eradication must be re-evaluated if medfly populations were not driven to extinction. Third, if the medfly is established and widespread in the Los Angeles Basin, measures can be taken to inhibit its spread to the main agricultural regions within the state as well as to other states.

The underlying conceptual framework distinguishing the two hypotheses is presented graphically in Fig. 1. Under the reintroduction hypothesis, denoted model 1, medfly invasions are held to be relatively common and that invading populations rapidly and without interruption develop or pass through each of the main phases—introduction, colonization, naturalization, and spread. It is assumed further that populations are detected in the earliest stages of invasion (after one to three generations) and that eradication efforts are effective in driving the population to extinction with no residual or outlying colonies remaining.

Under the alternative hypothesis, depicted in Fig. 1 as model 2, it is assumed that the medfly captures in southern California stem from an established, low-density population and that medfly invasions are rare. However, once an introduced population survives through the critical early phases, its growth may be slow and sporadic in the short term but persistent and inexorable in the long term. Therefore, according to this model, populations may not be detected for years after establishment. This model also suggests that eradication efforts may reduce populations to levels similar to those occurring in the early stages of colonization, but these will eventually build back up to detection levels.

In this article, I examine the question of whether the medfly is established in California. To do this, I use the two sets of available data—historical medfly captures in southern California and interception data at potential entry pathways (*3*).

Medfly Captures in the Los Angeles Basin

Numerical and seasonal patterns. Data on all adult medfly captures in southern California were obtained from the California Department of Food and Agriculture (CDFA). The numbers of medfly adults captured in southern California each year are given in Fig. 2. No medflies were found in the state before 1975. From 1975 through 1985 medflies were captured intermittently, and from 1986 through 1990 they were captured each year. A total of 279 medflies were captured in the most recent outbreak from July 1989 through November 1990. At least one medfly was captured in all but one month during this period, including two female medflies captured one week after eradication was declared.

The inset in Fig. 2 gives the monthly distribution of medfly captures. No medflies were captured in the period January through May until 1990. Of the 516 adults captured in southern California, around 92% were captured in the summer-fall period (July through December) and about 8% were captured in the winter-spring period (January through June). Nearly half of all captures were in September and October.

Spatial patterns. The general locations of medfly finds in 1975 through 1990 are shown in Fig. 3. Several aspects of the spatial components of these outbreaks merit comment. First, the area over which medflies were found was considerable. The total area treated

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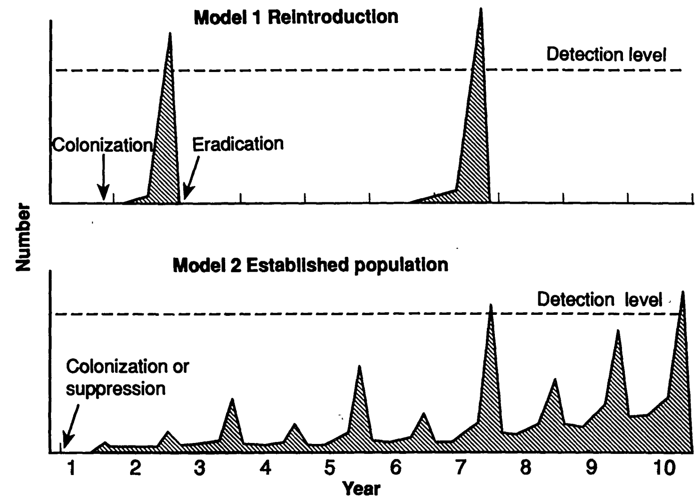

Fig. 1. Diagram illustrating patterns of medfly colonization and growth according to two alternative invasion models.

in 1989 and 1990 alone was over 600 square miles. Medflies were found as far apart as 70 miles ranging from Northridge, Resida, and Sylmar in the northern and northwestern parts of the Los Angeles Basin to the cities of San Bernardino and Riverside in the eastern part. Medflies were captured in a total of 73 cities in the greater Los Angeles area. A medfly has been discovered in about one out of three cities in Los Angeles County.

Second, medflies were recovered in two or more separate years in each of eight cities in the Los Angeles Basin, including Baldwin Park (1981 and 1989), East Los Angeles (1987, 1989, 1990), La Puente (1981 and 1989), Los Angeles (1975, 1982, 1987, 1988, 1989, and 1990), Northridge (1980 and 1988), Resida (1980 and 1988), West Covina (1981, 1989, and 1990), and Westminster (1987 and 1989). In virtually every city the recent captures were within several blocks of captures in earlier years. All of the cities that were infested in the early 1980s were reinfested in the late 1980s.

Third, medfly captures have been completely absent near the international points of entry. These points include Los Angeles International Airport near Santa Monica Bay and Los Angeles and Long Beach Harbors at San Pedro Bay.

Fourth, discoveries have been moving mostly eastward but also south and north from the original finds in the Culver City area. The population could obviously not spread west due to the Pacific Ocean. In 1980 the eastern boundary was still confined to the city of Los Angeles. In 1981 the eastern boundary was Baldwin Park and by the end of 1989 the eastern boundary was San Bernardino County.

Several more medflies were captured in neighboring areas in 1990 before the eradication declaration. The two flies found the week after this declaration were both in San Bernardino County. Recent detections in the eastern counties of the Los Angeles Basin were not due simply to increased trapping efforts in that Riverside, Orange, and San Bernardino counties have always maintained approximately the same fruit fly–trap densities and protocols as neighboring Los Angeles County.

Interceptions Along Major Entry Pathways

Airport interceptions. The U.S. Department of Agriculture (USDA), Plant Protection and Quarantine, maintains records at all international airports nationwide of fruit fly interceptions resulting from the day-to-day airport inspections and monitoring. Computerized printouts of interceptions for four groups—*Anastrepha* sp., *Bactrocera* sp., unidentified fruit flies, and *C. capitata*—were obtained from the USDA Biological Assessment and Taxonomic Support unit in Hyattsville, Maryland, for the period 1985 through July 1990.

The number of medflies and other major fruit fly groups that were intercepted at California airports by the USDA Plant Protection and Quarantine personnel in the period 1985 through July 1990 is shown in Fig. 4. This figure reveals one extremely important point—there were only five medfly interceptions in all three California international airports during the 5- to 6-year period—four in Los Angeles, one in San Francisco, and none in San Diego. Yet in the same period there were over 4000 interceptions of other fruit flies. That medfly interceptions are rare is corroborated by the results of intensive searches of baggage and cargo at airports presented in the following section.

Airport blitzes. Because both CDFA and the USDA felt that many medflies were being introduced to California through cargo and passengers through the two main international airports in California, three intensive searches involving 100% inspections (these were referred to as blitzes) of passenger baggage and two searches of air cargo were conducted in the period 14 May through 31 August 1991 at Los Angeles and San Francisco International Airports (*4*). Flights were targeted from all regions of the world considered high medfly risk, including South and Central America, Africa, the Middle East, Hawaii, and the Mediteranean region of Europe.

No medflies were discovered in any of the five 1-week blitzes (Table 1). The results basically confirmed the findings of the long-term routine inspections of in-coming passenger baggage conducted by the USDA—very few medflies are entering the state by way of airline passengers or on cargo shipments from countries where the medfly is established.

Fruit fly interceptions at border stations. The California exclusion program involves 16 border stations that operate on all major roads leading into the state (*5*). Records for fruit fly interceptions including the medfly at all stations since 1974 were obtained from CDFA. There were only two medfly interceptions in the 16-year period. In general, the infrequency of medfly interceptions at border stations strongly suggests that medfly introduction by infested fruit brought in by vehicles is minimal.

Interception in mail. To determine whether first-class mail was a

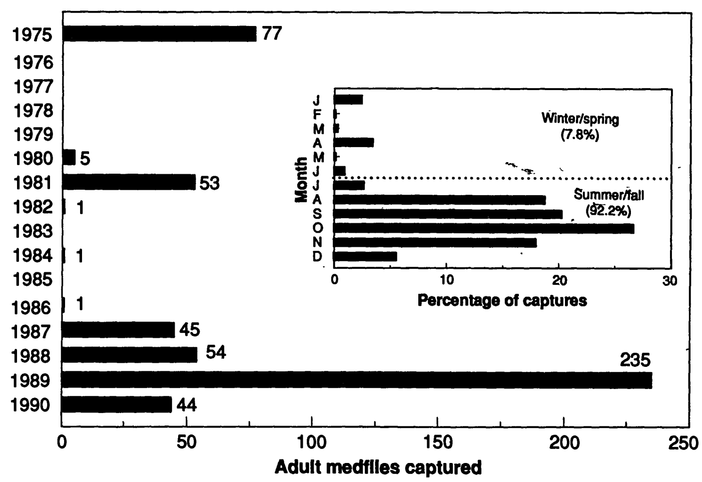

Fig. 2. Adult medfly captures by year from 1975 through 1990 and frequency distribution of all captures by month (inset).

source of medfly introductions into California, the USDA and the U.S. Postal Service agreed to a pilot program in which first-class mail would be inspected under search warrants for prohibited agricultural products during a trial period. A cooperative pilot program began 22 May 1990 at the main post office in Honolulu, Hawaii (*6*). Results presented here include the findings from June through October 1990. A total of 1.5 to 2 million postal packages were processed during this period.

A total of 29 packages of mail were found to contain fruit fly–infested host material. Five of these contained medfly larvae destined for three California locations: Sacramento in northern California, Long Beach in Los Angeles County, and Westminster in Orange County. Three of the packages were from the same source in Hawaii and destined for the same address in Sacramento. The remaining interceptions were of *Bactrocera* sp. (22 packages) or unidentified tephritids (2 packages). The results demonstrate that first class mail from Hawaii represents a means of transport for medfly larvae to California but that the rates are low.

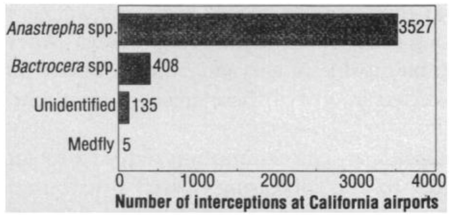

Fig. 4. Fruit fly interceptions from 1985 through July 1990 at the three international airports in California: San Francisco, Los Angeles, and San Diego.

Model Evaluation: Observations and Model Predictions

Five basic patterns emerged from the data analysis—scarcity of interceptions, seasonality, year-to-year captures, reappearances in the same regions, and eastward spread. The assumptions required by the models to explain each of the patterns are briefly discussed below.

Scarcity of interceptions. Medfly-infested fruit entering California is a necessary but not a sufficient condition for medfly establishment. This is because flies must complete the sequence of steps leading to complete establishment, of which introduction is only the first. The enormous difficulty of finding medfly-infested hosts along any of the pathways into the state strongly suggests that medfly introductions are rare. For example, the low number of medfly interceptions at border stations (total of two), if viewed in isolation, might be explained as due to the inefficiency of vehicular inspections (although the stations intercepted thousands of related fruit fly species). Or the findings of only five medfly interceptions in six years in all California airports resulting from routine baggage inspections might also be explained as due to inefficiency. Or the complete lack of medfly interceptions resulting from the 100% searches of baggage from 62,000 passengers originating from dozens of high-risk regions such as Hawaii, South America, Europe, and Africa might be explained as due to the wrong time of year, wrong flights, inefficiency of search, and so forth. But it is extremely difficult to explain away all of them. Indeed, the results of one approach reinforces that of the other. To explain the rarity of medfly interceptions into the state by model 1 requires the assumption that some unknown pathway into the state exists. On the other hand, the rarity of medfly interceptions and the lack of medfly captures near international ports of entry reinforces model 2 because this model does not require new medfly introductions to explain the reappearances of medflies.

Seasonality. Medfly appearances in southern California as well as in similar areas where the medfly is established are primarily in the late summer and fall months. The assumptions necessary to explain this trend by the model 1 (that is, reintroduction) include one of the following: (i) medfly introductions always occur before the summer and fall and therefore massive population growth occurs in early summer or fall just prior to detection; or (ii) medfly colonization occurs nearly every year somewhere in the Los Angeles Basin but requires several years to build up to detection levels. The assumption necessary for this pattern of seasonality to be explained by model 2 (that is, established population) is simply that the resident medfly populations follow seasonal patterns that are similar to those in all Mediterranean regions—mostly quiescent or inactive in the winter and spring and active in the summer and fall. Annual disappearances of medflies may have as much to do with seasonal aspects of their biology as with the consequences of eradication procedures.

Year-to-year captures. A number of unrealistic assumptions must be invoked to explain the year-to-year medfly captures by the reintroduction hypothesis. The required assumption is that each of the four main phases of invasion must occur not only year after year but also be completed in an extremely short time period. Evidence from studies on deliberate introductions of species in biological control suggests that colonization is often extremely difficult for any species even under the most ideal conditions (7). The assumption required to explain this pattern of yearly captures by model 2 is simply that local conditions vary each year and some areas are more conducive to growth than others.

Reappearances in same regions. This aspect involves various spatial scales ranging from the Los Angeles Basin to local neighborhoods. The central component of this pattern pertains to the fact that medflies reappear almost exclusively in the Los Angeles Basin and not other large metropolitan areas, primarily in Los Angeles County and, until recently, not even adjacent counties. They were also within four to six blocks of where they were found previously in cities and neighborhoods. Demographic and ethnic arguments must be invoked to support model 1 by assuming that certain ethnic groups are more prone than others to continually mail or carry in medfly-infested hosts. But the demographic analysis of the infested and noninfested areas does not bear this out (*8*). For example, there are roughly 13.5 million people in the greater Los Angeles area. If introductions were due to chance alone and weighted according to number in population, then for every one infestation in the Los

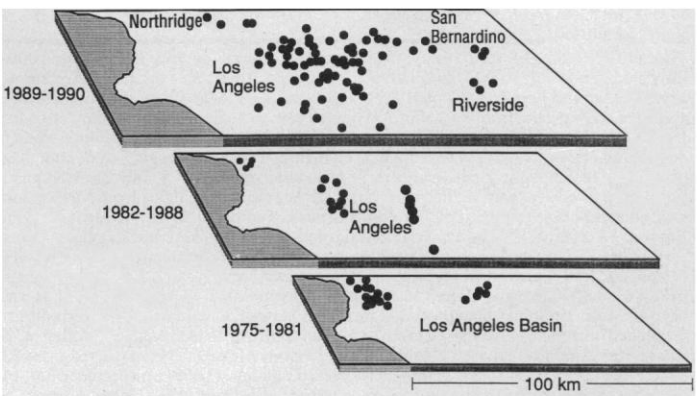

Fig. 3. Location of adult medfly captures in the Los Angeles Basin from 1975 through 1990. Each point represents a location of medfly captures but not necessarily the location of each individual medfly.

Angeles Basin there should be one for every 13.5 million people elsewhere along the southern U.S. border in areas where the medfly is thought to be capable of surviving. Yet only one infestation has ever been detected in any of these areas—a small one in Texas in 1966.

Eastward expansion. The assumption required to support model 1 with respect to the increasing spatial distribution of medfly captures is that there must be specific reasons for introductions to start appearing only recently in areas adjacent to where the medfly had previously been found but, at the same time, not in areas distant from previous finds. However, the assumption required to explain this pattern according to model 2 is simply that it is the evidence of the resident population expanding to new adjacent areas.

Model Evaluation: Absence of Population Explosion

A question that was frequently discussed among members of the CDFA Medfly Advisory Panel for the 1989–90 eradication program was why the medfly populations had never truly exploded given the species' enormous biotic potential (*9*), the widespread host availability in the Los Angeles area, and the apparent lack of population constraints. Indeed only 516 adult medflies have been captured in the entire Los Angeles Basin. There are several interrelated reasons why this situation could exist. First, few populations are ever truly unconstrained including newly introduced ones. For example, the majority of medfly larvae dies before pupating even when growing on primary hosts; generalist predators such as ants, carabid beetles, and spiders certainly take a large toll; and climatic factors such as extremes of heat, cold, and precipitation frequently suppress population growth. Second, medflies are often relatively rare in regions where they have been introduced but are now permanently established including Central and South America, Europe, parts of Africa, and Hawaii (*10*). This is in spite of apparently abundant hosts and tropical climates. Third, many invading pests with high population growth potential required decades to become widespread. Examples include the spread of the gypsy moth in Massachusetts in the mid-1860s as well the Japanese beetle in the early part of this century, which spread only 3 square miles in 6 years in the early stages of its invasion (*11*). Fourth, aerial malathion spraying does severely suppress medfly populations in areas where this method is used for control such as in Israel (*12*). More than 1000 square miles in the Los Angeles Basin have been treated with malathion bait sprays for medfly eradication from 1975 through 1990. There is little doubt that these efforts significantly reduced medfly populations in the region.

Invasion as a Cancerous Process

It is clear from the findings that an ecological invasion is a process and not a single event. The medfly invasion can be described as cancerous in that its development was latent, insidious, chronic, and persistent. Cancer serves as a useful analog in conceptualizing ecological invasions. Initial formation of cancer cells from which tumors arise corresponds to the introduction and colonization phases (*13*). Populations before detection are similar to the population of cancer cells in the latent, preclinical phases of tumor growth (*14*). A long pre-detection period allows medfly populations to spread prior to intervention so that "early" detection only occurs after substantial population growth. Once firmly entrenched, the parent tumor (originally medfly colony) may undergo metastasis—the spread of cells (medflies) to noncontiguous sites and establishment of secondary growths (satellite colonies). Phases of spread correspond to many stages of the "metastatic cascade"—a series of sequential steps starting with detachment of cancer cells (medfly dispersal) and ending with establishment of metastases in new organs (habitats). Like detached cancer cells, medflies that complete all the steps to establish new colonies have survived a demanding sequence of hostile events that undoubtedly kill the majority. Malathion-treated regions of Los Angeles may contain small residual pockets of medflies that are capable of population regeneration in the same way that "cured" tumors contain subpopulations of stem cells that can regenerate the tumor after treatment.

This analogy with cancer provides insights into reasons for the heterogeneous distribution of the medfly in the Los Angeles Basin, highlights the difficulty and inefficiency of establishment of new medfly colonies and helps explain how the pest became widespread in spite of aggressive trapping and seven separate eradication programs. The parallel also fosters integration of concepts from epidemiology, particularly with regard to eradication. For example, a distinction in epidemiology is made between three steps or grades: control, elimination, and eradication (*15*). "Elimination" is conceived as elimination of the disease (medfly problem) but not the pathogen (medfly); "eradication" is the purposeful extinction of the pathogen (medfly). Elimination is to eradication in medfly programs as remission is to cure in medicine. The distinction between eradication and elimination is not a fine point. If procedures have to be continued to prevent regeneration of an established medfly population, then the state is one of control and not eradication.

Table 1. Results of 100% baggage and cargo inspection in 1990 reported by CDFA of targeted flights at two major international airports in California—Los Angeles International Airport and San Francisco International Airport.

Airport	Number checked	Mexican fruit fly group (*Anastrepha* sp.)	Oriental fruit fly group (*Bactrocera* sp.)	Unidentified	Medflies (*C. capitata*)
		Passenger			
LAX*	16,997	49	2	5	0
LAX†	34,393	14	3	2	0
SFO‡	10,341	0	2	1	0
		Cargo shipments			
LAX§	1,387	0	0	1	0
SFO‖	1,043	0	0	0	0
Total		63	7	9	0

*Conducted from 14 to 20 May; baggage from a total of 153 flights was 100% inspected involving 16,997 passengers from South American countries (Argentina, Brazil, Chile, and Ecuador), Central America (Costa Rica, El Salvador, and Guatemala), and Mexico; baggage from a total of 337 flights was partially inspected from Australia, Japan, Philippines, Iran, Korea, Malaysia, Taiwan, and Thailand; baggage subjected to dog teams from seven Hawaii flights involving 1,738 passengers and complete inspection of 83 flight crew members. †Conducted from 29 July to 4 August; original targeted area was Mediterranean though later included flights from Mexico and Central and South America.Total of 48 countries including Australia, Mexico, 15 from Europe, 13 from Africa, and 6 each from Central and South America. Baggage from a total of 34,393 passengers on 163 flights was given 100% inspection as were 2,084 passengers on 8 flights from Hawaii. ‡Conducted from 19 to 25 August; baggage from a total of 10,341 passengers on 49 flights was subjected to 100% inspection as was baggage from 1,686 passengers on 6 flights from Hawaii. Countries from which flights originated included Australia, Mexico, 15 from Europe, 7 from Central America, 6 from South America, 7 from the Middle East, 13 from Africa. §Conducted from 23 to 27 July; a total of 1,387 shipments were completely (100%) inspected from 44 countries including Australia, Mexico, 14 countries in Europe, 6 in Central America, 5 in South America, 11 in Africa, and 6 in the Middle East. ‖Conducted from 27 to 31 August; total of 1,043 shipments were completely inspected from Hawaii and 55 different countries including Australia, Mexico, 15 countries in Europe, 7 in Central America, 6 in South America, 14 in Africa, 3 in the Middle East, and 3 in Asia-Pacific.

Implications

Many important aspects of medfly eradication programs change when they are based on the underlying assumption that the pest is established. For example, current protocol for CDFA's medfly action plan calls for treatment when a detection is made of any of the following (*16*): (i) two flies within a 3-mile radius and within a time period equal to one life cycle of the fly; (ii) one mated female; or (iii) larvae or pupae. A protocol based on the assumption that the medfly is established would place sole emphasis on strict presence of the flies rather than on mating status, sex, life-cycle duration, distance between captures, or number captured. Likewise, detection protocols call for high density trap grids to be maintained for two generations after eradication is declared. However, due to the seasonality of medfly finds (that is, mostly summer-fall), a large part of the time in which these intensive trapping programs are conducted includes the period of lowest abundance of medflies (that is, winter-spring). Because timing for decision-making is based on duration of the medfly life cycle which, in turn, is based on temperature accumulation (degree-day) models, termination of the high-density trapping almost always occurs during the period when medfly populations are most inactive; in other words, during a time when medflies are least likely to be captured even when present. Sound trapping protocols and interpretation of captures based on the assumption that they are established would place much more emphasis on a consideration of seasonality rather than on temperature models.

There are two aspects of the science of invasions that are seriously lacking in the analysis of virtually all medfly invasions. First, genetic information on the medfly in California is totally absent. Field protocols do not include provisions to preserve adult or larval specimens for analysis. Yet an enormous amount of useful information could be extracted from a genetic library of the medfly in California if material were available. This includes information on genetic changes that occur during colonization, worldwide source of established medflies, relatedness of flies caught in different years and between near and distant locations in the Los Angeles area, the local and regional effects of post-eradication bottlenecks, the possibility of secondary invasions, and insights into the effects of selection and drift on population adaptations. Second, the population biology of the earliest parts of the colonization phase of invasion is poorly understood for all fruit fly species. Understanding the biology of fruit flies is a related but fundamentally different problem than understanding the biology of fruit fly invasions. Yet millions of dollars in eradication program costs hinge on a putative understanding of this invasion process.

The short-term medfly situation in southern California is expected to follow recent seasonal and annual trends—several years with only a few flies captured or minor outbreaks with infrequent massive outbreaks similar to the 1989–1990 outbreak; most of the flies will be captured in the summer and fall with few or none captured in the winter and spring. It is impossible to predict the exact year and location of future outbreaks although new flies will surely be found in San Bernardino, Orange, and Riverside counties as well as in areas of Los Angeles County previously infested. There is little doubt that major outbreaks in southern California will occur in the future. The possibility also exists that the medfly has already spread beyond the Los Angeles Basin.

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