

# Short- and long-range dispersal of medfly, *Ceratitis capitata* (Dipt., Tephritidae), and its invasive potential

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**Abstract:** Data were obtained from mark recapture trials pertaining to the dispersal of medfly, *Ceratitis capitata* (Dipt., Tephritidae), over both short (10–160 m) and very long distances (0.5–9.5 km) within the surveillance trapping array in Adelaide, Australia. They could be related to previously reported data sets by expressing the capture rates of each set in common terms that corrected for differences in recapture rate resulting from type of trap, season or climate. The mean capture rate at each distance from the point of release in each data set was expressed as a percentage of the real or inferred rate of that set at a distance of 100 m. The resulting distribution of dispersal distances conformed to both an inverse power model and a modified Cauchy model regardless of whether the present and previous data were combined or not. The modified Cauchy model inferred that the median distance flown was extremely short and 90% of flies displaced only 400–700 m despite the fact that a consistent trend in declining catch rates was obtained up to 9.5 km. The spread of invading propagules in quarantined zones in the first generation is likely to be limited by a decline to non-viable density within 1 km or less of the incursion point and the spread of larger infestations could be limited by the longevity of the dispersers. The results also have significance to the ability of surveillance trapping arrays to detect infestations and also to methods of distributing insects for the ‘sterile insect technique’.

**Key words:** *Allee effect*, Cauchy, power distribution, quarantine, surveillance, trapping

## 1 Introduction

There have been many investigations of dispersal in the Mediterranean fruit fly (medfly) *Ceratitis capitata* (Wiedemann) (Dipt., Tephritidae). Most have involved release of marked flies from a point and recapture by traps set at different distances and directions from that point (Wakid and Shoukry 1976; Wong et al. 1982; Baker and Chan 1991; Plant and Cunningham 1991; Barry et al. 2002). Others have involved releasing flies at different distances and directions from a central trap (Cunningham and Couey 1986; Lance and Gates 1994). This degree of attention is not surprising, because the species is the most widespread and economically significant pest in its family (White and Elson-Harris 1994) and dispersal ability is pertinent to the design of surveillance trapping programmes and the ability of the pest to establish new propagules (Cunningham and Couey 1986; Plant and Cunningham 1991; Lance and Gates 1994; Meats 1998a). Dispersal is also relevant to the population control of pests through the mass release of sexually sterilized con-specific individuals (the ‘sterile insect technique’, SIT), because too little dispersal could result in uneven coverage of the target

area or even no coverage of some patches of it (Meats et al. 2006), whereas too much could mean that sterile individuals would be wasted if they rapidly left the target area.

The frequency of movements over long distances can be important in determining the rate of spread of invasions (Neubert and Caswell 2000; Gilbert et al. 2004; Hastings et al. 2005; Muirhead et al. 2006). However, the chances of an incipient propagule establishing itself can depend on most dispersal distances being short so that a sufficient density of individuals remains around the point of introduction (Bateman 1977; Hopper and Roush 1993; Kot et al. 1996; Veit and Lewis 1996; Meats 1998a; South and Kenward 2001; Hastings et al. 2005; Meats and Clift 2005; Taylor and Hastings 2005). Both conditions can be met when the distribution of dispersal distances (DDD) has a ‘fat tail’, whereby the rate of fall in frequency at longer distances is relatively low (when compared with the predictions of a negative exponential model), because it conforms instead to an inverse power model (Fletcher 1974; Mayer and Atzeni 1993; Hill et al. 1996; Meats 1998b; Roslin 2000; Paradis et al. 2002; Finch and Collier 2004; Winkler et al. 2005).

A suitable inverse power model has the form  $y = ax^{-b}$ , where  $x$  is distance from the point of origin (such as the nest site of fledgling birds or the emergence or release point of adult insects), and  $a$  is a scaling constant (adjusting the height of curve). Such a model, however, is unrealistic for very low values of  $x$ , because it can predict very high values around the point of origin, which have not been observed. A Cauchy distribution (which resembles a half-normal distribution but with a flatter top and a fatter tail) is more plausible because its slope is zero at the point of origin and gradually increases with distance to stabilize as an inverse power relationship (Mayer and Atzeni 1993; Clift et al. 1998; Paradis et al. 2002; Winkler et al. 2005).

Almost all the releases of medfly to date have involved flies from laboratory culture. This is necessary if large numbers are required of the same age; this may be deemed desirable because dispersal tendency can vary with age or physiological state (Johnson 1969) and the tail of the DDD may be undetectable if small numbers are released (Southwood and Henderson 2000). It is always possible that laboratory insects may not disperse in the same way as wild ones, but in the case of medfly, Wong et al. (1982) found very little difference in the DDDs of *C. capitata* of wild and cultured origin.

Despite the large number of studies on the dispersal of *C. capitata* (cited above), it is not immediately apparent that any conclusion can be made about the form of the DDD. One reason for this is that suitable data have been published only for very limited ranges of distance and for none with a range having a maximum exceeding 700 m. Another probable reason is that overall recapture rates have varied, probably because releases have been made in different parts of the world, in different seasons and using different kinds of trap. We report data pertaining to the dispersal of medfly in Adelaide over both short (10–160 m) and very long distances (0.5–9.5 km) and relate them to previously reported findings from other locations by means of novel methods of comparison.

## 2 Materials and Methods

### 2.1 Production and marking of flies

The releases were of 'males only' which was possible through the use of a genetic sexing strain (Vienna 7 Mix 99) in which female eggs could be killed by exposure to a mild heat stress that did not affect males (Franz et al. 1996). The Western Australian Department of Agriculture in Perth produced the pupae, which were sterilized with 180 Gy gamma irradiation from a  $^{60}\text{Co}$  source and air-freighted to Adelaide. They were marked (Steiner 1965) with fluorescent powders (Fiesta ®; FEX Series, Swada, London, UK) and allocated to paper bags (14 g in each) and each bag was placed in a 5-l cardboard tub with 40 ml aqueous gel of agar (0.6%) and sugar (18%), with the preservative methylparaben (0.01%). The tubs were held at 25°C, 65% r.h., and L14 : D10 until release 3 days later. The number of flies that actually flew from the release site ('fliers') was estimated from concurrently run standard quality control tests for flight ability (FAO/IAEA/USDA 2003).

### 2.2 Recapture of dispersed flies in Adelaide

Adelaide is well suited to dispersal studies because it has a surveillance grid of approximately 3750 medfly traps spaced 0.4 km apart over an area of about 600 km<sup>2</sup>. Flies were recaptured in Lynfield (pot) traps of known GPS location that were baited with a mixture of 5 ml Capilure with 1% dichlorvos (Meats et al. 2002). The distance of each trap from any point can be determined from Pythagorean calculation. Catches were counted weekly after checking each trapped fly for traces of marker powder in the ptilinal suture using a microscope illuminated with blue light.

### 2.3 Types of data obtained in Adelaide

The DDD over a 'short' range (up to 160 m from the point of release) was measured at three sites (> 6 km apart), in the suburbs of Aberfoyle Park, Urrbrae and Morphettville, respectively, in November 2001. Releases were made at four different distances from a single trap at each site, flies at each distance being marked with a different colour. Over all sites, the total number of fliers released at each distance ranged from 6900 to 7400.

The DDD over a 'large' range (up to 10 km) was estimated from the recapture rate of flies at different distances from the boundary of the 23 km<sup>2</sup> treatment area of a large SIT trial that was centred in the suburb of Millwood (Meats et al. 2006), where a total of 38.8 million fliers was released over 12 weeks in the period September–December 2001. 7639 flies (0.02%) were trapped 1–10 km away from the boundary of the release area, and 224 flies (0.0006%) were trapped more than 10 km away. Because there was no way of knowing the exact point of origin of any fly (and therefore how far it had already displaced from it on leaving the boundary of the treatment area) the data were initially used to estimate the slope of the power model for the DDD and to confirm whether or not it applied over a span of 10 km. For this purpose, catches were grouped by distance, where a group was defined according to whether catches fell between 0–1 km, 1–2 km...9–10 km from the boundary of the release area. There were 107–201 traps in each group. The mean catch per trap (or a function of it) was then related to the mid point of these limits, that is 0.5, 1.5...9.5 km.

### 2.4 Two models for describing distribution of dispersal distances

An inverse power model has the form  $y = ax^{-c}$ , where  $y$  is the frequency of occurrence (or some function of it) and  $x$  is the distance from the point of release. The exponent  $c$  is found as the slope of the linear regression of  $\log_{10} y$  on  $\log_{10} x$  and therefore is best estimated over the range of distances over which the log-log relationship is obviously linear.

A modified model of the Cauchy distribution (Mayer and Atzeni 1993) was also used, having the form:

$$y = \frac{\alpha}{\beta\pi[1 + (x/\beta)^c]}$$

where  $\alpha$  is a scaling factor (adjusts the height of the curve) and  $\beta$  determines (but is not identical with) the distance at which the curve becomes congruent with the inverse power model having the same exponent  $c$ . The Cauchy distribution, as used by Mayer and Atzeni (1993), has  $c = 2$  with  $\beta$  being the median distance dispersed; when both  $\alpha = 1$  and  $c = 2$  the distribution is that of Student's  $t$  statistic with 1 degree of freedom (Patel et al. 1976).

## 2.5 Relating catch per trap to distance

The effects of differences in release rates between different sets of data can be removed by expressing the catch by each trap in any set as a percentage of the number of flies released. The effects of differences in both release rate and recapture rate in any data set can be removed by expressing the catch by each trap as a percentage of the catch at a standard distance (e.g. 0.1 km) from the release point. The data for short distances (0.01–0.16 km) could be treated in this way, but the only information obtainable from the set for long distance was the slope of catch with distance (as explained above). The data for short distances were expressed in terms of percentage of flies released, and the inverse power slope from the long distance data was fitted to them by using trial values for the intercept (made by applying trial multipliers to the long distance data). The notional value at 0.1 km was then obtained from the equation for the slope. The long-distance values adjusted by the multiplier giving the best fit (above) were assumed to be estimates of the catch per trap as a percentage of release from a single point.

## 2.6 Comparisons with other studies

Comparisons were made with other medfly recapture data published either as tables or graphs (Wakid and Shoukry 1976; Wong et al. 1982; Cunningham and Couey 1986; Lance and Gates 1994; Barry et al. 2002). Two methods were used. The first was to express reported catches as a percentage of the flies released (if they were not in this form already) and relate them to their corresponding distances from the release point. With the second method, catches were expressed as a percentage of the catch at a distance of 0.1 km from the release point. The notional percentages trapped at 0.1 km were estimated in each case by interpolation between the nearest two data points on either side of 0.1 km.

## 2.7 Statistical procedures

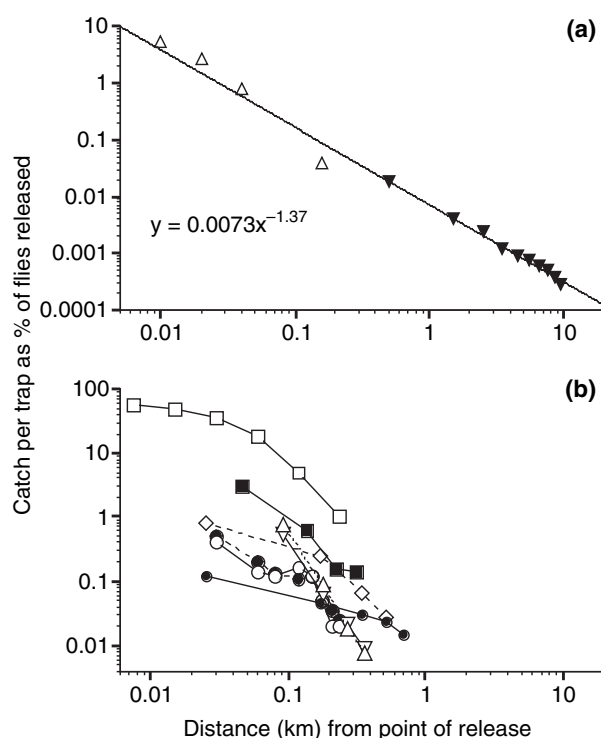
Standard procedures were used (Snedecor and Cochran 1989) as follows. The parameters of the power models were obtained from the slopes and intercepts of the linear regressions of  $\log_{10}$  catch data on  $\log_{10}$  distance (where catch data were expressed in the ways given above). Each power model was then used to predict the catch at the distance pertinent to each (untransformed) catch datum and the percentage of variance of untransformed catch data explained was found from the unexplained variance calculable from the deviations of the predictions from the real data and the overall variance of the latter.

The best fitting Cauchy distribution was found by using trial combinations of  $\alpha$  and  $\beta$  to obtain the lowest deviations of data from model; the percentage of variance explained in each case was obtained from the unexplained variance calculable from those deviations and the overall variance of the catch data.

## 3 Results

### 3.1 Distribution of dispersal distances

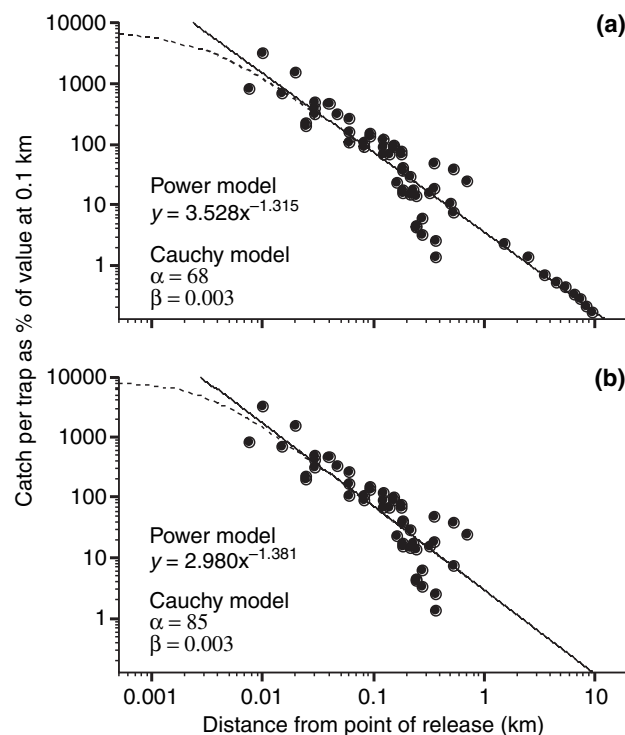
The relation of catch per trap (as percentage of flies released) to distance from release point could be fitted to a power curve of slope  $-1.367$  for the Adelaide releases (fig. 1a), although the long-distance series is scaled (with a height adjustment) to fit the other one



**Fig. 1.** Relation of catch per trap to distance from point of release when catch per trap is expressed in terms of percentage of flies released. Unless where mentioned otherwise, releases were of both sexes and recapture rates pertain to the male component of the release. (a) Adelaide (current) results with male-only releases. (b) Results elsewhere, (previously published). Symbols on (a): white triangles pertain to known short distances; black triangles pertain to flies trapped at different mean distances from the boundary of an area of mass releases. Symbols on (b): white squares (Cunningham and Couey 1986); black squares (Lance and Gates 1994); white triangles and inverted white triangles, both sex and male only releases respectively (Barry et al. 2002); white and black discs, wild and sterile flies respectively (Wong et al. 1982); black dots and white diamonds, winter and summer releases respectively (Wakid and Shoukry 1976)

because the effective number released was not known. The relationships obtained from other studies all pertain to a limited range of distances and vary widely in terms of steepness of slope and linearity (fig. 1b). When catch per trap is expressed as a percentage of the estimated value at 0.1 km, the combined data conform to a power curve of slope  $-1.315$  (fig. 2a). If the Adelaide long-distance data are removed (because of doubts about the assumptions on the point of origin of the trapped flies) a very similar slope of  $-1.381$  is obtained (fig. 2b).

There was no evidently biased deviation of trend at shorter distances and consequently both inverse power and Cauchy models could be fitted equally well. For the full data set, the percentage of the variance explained by the power and Cauchy models amounted to 58.2 and 58.6 respectively. For the data set without the long-distance recaptures, the equivalent



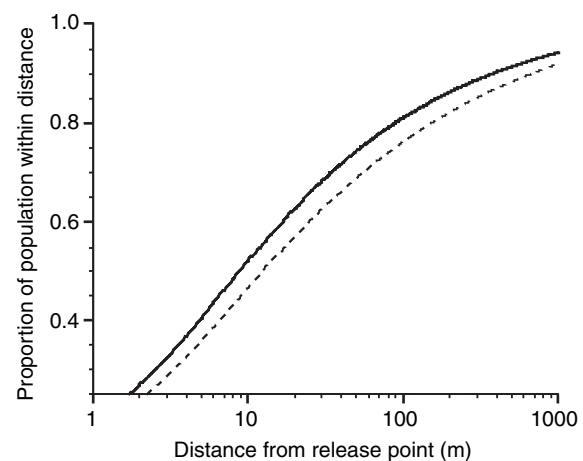
**Fig. 2.** Relationship of catch per trap to distance from point of release: (a) all data, (b) excluding long-distance Adelaide data. Catch per trap expressed in terms of percentage of that at 100 m. Inverse power model, solid line, Cauchy model, dashed line

percentages of variance explained were 62.3% and 66.2% respectively. For both data sets, the value of  $\beta$  giving the best fit for the Cauchy model was 0.003. When a Cauchy model has an exponent of 2, a value of  $\beta = 0.003$  would indicate a median distance of dispersal of 3 m (Mayer and Atzeni 1993). However, because the exponents here were 1.315 and 1.381, the median distance was estimated by using each Cauchy model to calculate fly frequency at 0 m and at every metre up to 12 km; it was then apparent that half the flies would occur within 12.5 m of the release point if the model based on the full data set was correct whereas if the other model was correct the pertinent distance would be about 8.5–9 m.

Figure 3 shows the mean expectations of the models in fig. 2a (dotted line) and 2b (solid line) in terms of the proportion of flies within any given distance up to 1 km. For instance, depending upon which model we use, we can expect 90% of flies will remain within about 400–700 m. The results are similar to the complex model of Plant and Cunningham (1991) particularly, for proportions over 0.8.

#### 4 Discussion

The advantage of using the Cauchy model is that it is possible find the distance within which any proportion of such a distribution would, on average, be expected to fall. This, in turn, is a ready way of visualizing and quantifying dispersal tendencies. However, the significance of such traits depends upon their associated risks



**Fig. 3.** Accumulated frequency curves derived from the Cauchy distributions given in fig. 2. Dashed line from fig. 2a, solid line from fig. 2b

and benefits. The benefits of long-distance dispersal would include the opportunity to outbreed, and to spread the chances of survival over several habitat patches whereas the risk is well illustrated by Whitmore and Tobin (2006) who found that persistence of incipient gypsy moth propagules ahead of the main invasion front in North America was by no means guaranteed and survival was variable from place to place. Likewise, adventitious introduction by human agency (jump dispersal) does not always lead to establishment; Meats et al. (2003) found that 71% and 18% of incipient incursions within surveillance trapping arrays of Queensland fruit fly and medfly, respectively, did not establish to a stage that warranted insecticidal or other treatments.

There can be many reasons for a failure to establish a population at the fringe of a distribution. Stiling (1993) reviewed failures in the introduction of beneficial organisms for biological control and found that the three main reasons given were related to climate (34.5%), predation or parasitism by native fauna (20.3%) and lack of alternative hosts or food (16.9%). Some failures may be due to the disadvantages of being an isolated and small population. Such a population (whether of a recently arrived propagule or of a rare and endangered species) would be vulnerable to random probabilities of extinction and problems of inbreeding (e.g. see Dennis et al. 1991; Caughley and Sinclair 1994). In addition, there may be problems that can be grouped collectively under the 'Allee effect' which is manifest as a low or even negative rate of increase when a population is at a very low density and may be due to one or a number of phenomena caused by low density such as reduced abilities to find mates, survive, grow and rear offspring (Allee 1931; Allee et al. 1949).

So how is dispersal related to the risks of medfly spreading naturally to adjacent regions that have the resources (fruit) to support it? We have shown that medflies can disperse over a long distance of their own accord, but that only a tiny proportion is likely to do so. Moreover, dispersal to a given distance depends

upon the disperser's ability to survive long enough to get there, thus even in the absence of environmental causes of death (such as predation or bad weather) there will be an intrinsic limit imposed by maximum potential lifespan. The Cauchy distribution is leptokurtic and the tail, by obeying an inverse power law, is theoretically infinite, diminishing in a scale-invariant manner. In the case of progeny arising from an invading propagule it is axiomatic that somewhere, at some distance from the origin (say distance A), the density will have declined to an Allee limit and further out (at distance B) there will be a point beyond which even the most longevel individual cannot reach due to lack of time (hence the real DDD would be truncated at this point). For an invading propagule, dispersal of unmated insects beyond A is not adaptive but a female that mated within distance A could carry fertile eggs out to any distance that could be achieved in its lifetime. It remains to be established whether this has significance to the spread of an incursion because it is not known whether a single female could deposit enough eggs in one place to give rise to another propagule of viable size. However, with a bigger source population (such as a heavily infested town), many fertile females would disperse out and impose a high rate of arrival of incipient propagules (propagule pressure) on any adjacent uncolonized regions. But what sort of distance from a highly infested would reduce the risk of contagion to a low level? We do not know how long medfly can survive in the field or what its daily rate of displacement may be, but an estimate of 1 km per day for 21 days would infer that the potential reach of even a very dense infestation would be limited to 21 km.

At the other extreme, most medfly do not disperse far and this has significance for the effectiveness of both surveillance trapping arrays and SIT. The Cauchy model used here predicts fewer flies around the origin than does the inverse power curve, yet it still implies that most flies will remain within a few tens of metres of where they are put (or from the point of emergence in the case of a natural propagule) and that 90% would remain within about 400–700 m. This will mean that surveillance trapping arrays may not detect some incursions in their first generation if the traps are spaced further apart than about 400 m (Cunningham and Couey 1986; Lance and Gates 1994) and that small propagules are unlikely to spread further than 1 km (Meats et al. 2003). It also means that when medfly is distributed for SIT, a wide dispersion must be achieved through the use of roving ground releases (Cunningham et al. 1980; Meats et al. 2006) or releases from aircraft (Nadel et al. 1967; Rendon et al. 2004) rather than through a series of releases at fixed points.

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