

Quantifying captures from insect pest trap networks

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- 1 Introduction
- 2 TrapGrid and other models to analyze trap networks
- 3 Applications
- 4 Practicum
- 5 Conclusion
- 6 Where to look for further information
- 7 Acknowledgements
- 8 References

1 Introduction

Networks of insect traps are created and maintained around the world for a variety of reasons. Here they are defined as a geographically dispersed set of traps, operated by a single entity, and for which catch data are collated. Among the most common goals of such networks, especially in the case of invasive pest insects, are surveillance, delimitation, and/or monitoring. In some cases, traps may be an important component of eradication programs. The goal of trap networks and the economics of their maintenance must be considered at every stage, since these drive design decisions, service schedules, analysis of captures, and the duration of the network's existence. Quantifying capture probability is extremely helpful for the design, continual optimization, and modification of these networks; there are models to allow this, of which TrapGrid is a recent example (Manoukis et al., 2014). Three examples of networks targeting insect pests include a high-density trapping program to eradicate *Lymantria dispar* in New Zealand, a delimitation network against Japanese beetle (*Popillia japonica*) in Missouri, USA, and an extensive network of traps for surveillance of multiple invasive species of Tephritidae in California, USA (Denning and Goff, 1944; Gray, 2010; Gilbert et al., 2013).

Surveillance networks are focused on minimizing the potential establishment of invasive species, which threaten natural ecosystems, agriculture, and economies globally (Paini et al., 2016). Surveillance networks enable early detection of a pest incursion, allowing cost-effective removal when tied to rapid response with effective measures to extirpate them (Simberloff et al., 2013). These sorts of networks were the original targets of TrapGrid development, but additional trap network types and goals are now also addressed by the model.

Delimitation surveys are often implemented after an invasive pest is detected, and may involve traps, especially when a more effective lure is available (FAO/IAEA, 2018; IPPC/FAO, 2018). Trap networks for delimitation have two goals: (1) confirm the presence of a population of the adventive pest and (2) determine the spatial extent of the population (van Havre et al., 2015). For many pests in the United States, a fully-trapped (fixed density trapping over a contiguous area) survey is often used, either an 8 km × 8 km or 14.5 km × 14.5 km grid (APHIS/PPQ, 2003, 2004), with the size determined by an expert assessment of the insect's vagility. In some cases, variable trapping densities are employed with the highest numbers of trap per unit area near the center of an incursion (usually assumed to be near where the first finds are made) and decreasing density in bands toward the edge (Caton et al., 2021a).

Trap networks for monitoring aim to provide information on the size of a pest population that is already established in the area. Often, timely reporting on this information is critical; an example of a monitoring network providing real-time information on pest pressure is the smart-trap network created by researchers in Taiwan targeting the oriental fruit fly *Bactrocera dorsalis* (Jiang et al., 2008). Monitoring is also frequently important as a component of integrated pest management programs (Vargas et al., 2008; Clarke et al., 2011) or provides evidence of 'low prevalence' of a pest, which can be a required first part of approved systems approaches (Quinlan et al., 2020).

Trapping as the only or principal tool of an eradication program is less frequent compared to trapping for surveillance and delimitation, since highly attractive, species-specific lures are required. In an eradication program, traps may be needed to assess progress. When an effective lure is available it may not be employed only in traps as part of an eradication; rather, mating disruption or male annihilation (MAT) might be deployed in eradication programs with such lures. In MAT, male attractants are used to target fruit flies and include a lure mixed with spot applications of insecticide in the affected area, rather than traps (Vargas et al., 2014). This saves cost (trap materials) and time (labor, handling time).

There are many combinations of traps and attractants employed in networks. For instance, the attraction and specificity of some of these might be very low; a set of yellow sticky traps may have visual attraction at a short range but draw in a large range of insect species. Similarly, food-based lures

are usually not highly specific. Other lure-trap combinations can be highly attractive to specific insects (Fig. 1).

The most effective lures are those related to or based on sex pheromones, paraperomones, or semiochemicals. For Lepidoptera, sex pheromones for more than 1600 species have been identified, and many are highly effective, e.g. 'disparlure' (2-methyl-7*R*,8*S*-epoxy-octadecane) for spongy moth (*Lymantria dispar*) (Bierl et al., 1970; Jurenka et al., 2003). Generally, these lures are based on sex pheromones produced by the female and can be highly attractive in small concentrations in the air, over large distances, to males.

Tephritid fruit flies are invasive pest insects of major economic importance around the world (White and Elson-Harris, 1992). A class of compounds sometimes called 'male lures' (which include paraperomones and semiochemicals) are particularly important for trapping many of these species (Shelly et al., 2014). Three commonly used products are 'trimedlure' (tert-butyl 4-chloro-2-methylcyclohexane-1-carboxylate; targeting the Mediterranean fruit fly, *Ceratitis capitata*) and the more attractive cuelure (4-(3-Oxobutyl)phenyl acetate) as well as methyl eugenol. Each of the last two attracts a variety of *Bactrocera* and *Zeugodacus* species, (Drew and Hooper, 1981). These lures are generally species-specific and can attract a large portion of the male population with such effectiveness as to eradicate a population via MAT (Steiner and Lee,



Figure 1 Cuelure-baited Jackson trap filled with melon fly (*Zeugodacus cucurbitae*) near Keaau, Hawaii. Though not the most attractive male lure, in an area of high prevalence it is possible to capture large numbers of males within an hour. *Photo by Nadya Kandel.*

1955). Quantifying the attractiveness of these lure/trap combinations via field experiments is critical to modeling trap networks.

The details of trap networks targeting fruit flies vary around the world. In the US state of California, the system is well-documented (Gilbert et al., 2013). There, fruit fly surveillance is the main goal, since California is the largest producer of fresh fruit in the USA and fruit fly establishment would cost billions of dollars in lost revenue in the first year alone (Suckling et al., 2016). Jackson traps, a type of small delta trap with a sticky card insert and lure (sometimes with insecticide) hanging inside are particularly widely used (Fig. 1). These may contain trimedlure (without insecticide) or methyl eugenol plus naled (1,2-dibromo-2,2-dichloroethylphosphate) or cuelure plus naled. In California, male lure-baited traps are supplemented with various protein-/food-based traps including glass McPhail traps with a torula yeast slurry, ChamP traps, Pherocon AM traps (yellow sticky panel) impregnated with ammonium acetate and protein hydrolysate, and multilure traps baited with BioLure (Quilici and Donner, 2012; Gilbert et al., 2013). The main fruit fly species of focus are *Ceratitis capitata*, *Bactrocera dorsalis*, *Bactrocera zonata*, *Anastrepha ludens*, *Bactrocera correcta*, and *Zeugodacus cucurbitae*. Other pest Diptera include *Anastrepha suspensa*, *Bactrocera correcta*, *Rhagoletis indifferens*, *Rhagoletis pomonella*, and *Zeugodacus cucurbitae*. Other pest insects also targeted by surveillance in California (but with different traps and lures) are Asian citrus psyllid (*Diaphorina citri*), boll weevil (*Anthonomus grandis*), European corn borer (*Ostrinia nubilalis*), European grapevine moth (*Lobesia botrana*), European pine shoot moth (*Rhyacionia buoliana*), Japanese beetle (*Popillia japonica*), and khapra beetle (*Trogoderma granarium*) (Gilbert et al., 2013).

2 TrapGrid and other models to analyze trap networks

2.1 TrapGrid model description

TrapGrid is a public domain, freely available software package that quantifies the probability of insects being captured by a network of traps baited with attractants. It implements a computer model published by Manoukis et al. (2014). Some of the important features of the model implemented by TrapGrid include the ability to set the attractiveness of each trap separately, set arbitrary trap positions and subsequent densities, model the dispersion of insects, and calculate capture probabilities over time. No model can include all the factors that may be relevant in the real-world situation, but it is anticipated that the most important features of many trap/insect systems are included and that running the model can lead to useful operational insight to improve network design.

A critical component of TrapGrid is the function that relates the distance of an insect from a given trap (calculated via the Euclidean distance, i.e. $d =$

$(x_0 - x_1)^2 + (y_0 - y_1)^2$ to the probability of its capture in that trap. In TrapGrid that function is the hyperbolic secant [*sech* (d, λ)]:

$$f(d, \lambda) = \frac{2}{e^{-\lambda d} + e^{\lambda d}}$$

Where d is the distance from the trap (usually in meters) and λ is a parameter that captures the 'attractiveness' of the lure/trap combination. Fig. 2 shows the probability of capture for varying values of attraction as a function of distance.

Attraction in the TrapGrid model is often presented as the reciprocal of λ . One reason for this is that smaller values of λ indicate more attractive lure/trap combinations, which can be counterintuitive. On the other hand, larger values of $1/\lambda$ mean a higher probability of individual insects being caught at a given distance. Moreover, $1/\lambda$ has real-world meaning and allows easy comparison of trap/lure combinations across insect species.

It is worth noting that other functions have been used to relate distance from a trap to the probability of capture in insects; these include exponential, logistic, or Cauchy distributions, for example (Cunningham and Couey, 1986; Plant and Cunningham, 1991; Meats and Edgerton, 2008).

Sech has some desirable properties for use in TrapGrid: First, the probability of capture is 1 when the distance from the trap is 0, which is clearly realistic

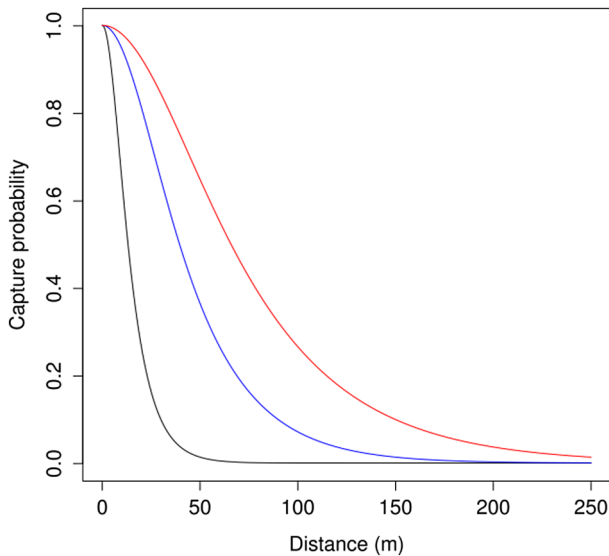


Figure 2 Capture probability as a function of distance from a trap following *sech* (d, λ). Lines represent traps of varying attraction: $1/\lambda = 10$ (black), 30 (blue), or 50 (red) m. *Figure from Manoukis et al. (2014).*

for a perfectly efficient trap (if the insect is in the trap, it is caught). Second, at a distance of $1/\lambda$, the probability of capture is a constant, about 0.65. This last feature makes it easy to compare the relative attractiveness of different lure/target species combinations. Fig. 3 illustrates capture probability surfaces for two traps, one with a low (Fig. 3a), ($1/\lambda = 15$ m) and one with high (Fig. 3b) ($1/\lambda = 35$ m) attraction. Clearly, the 'area under the surface' does not increase linearly with increasing attraction. The volume under Fig. 3b is much larger than might be expected compared with Fig. 3a. However, these numbers give a good 'real-world' idea of how effective a particular lure and trap are over space.

With the capture probability surface defined, it is possible to calculate the 'instantaneous capture probability' for an arbitrary grid. Visually, one can imagine an arena x_m by y_m meters (with area $A = x_m \times y_m$) in size with a height equivalent to the capture probability. If an arena contains a single trap (similar to one of the panels in Fig. 3), the probability of capture of an insect placed randomly in the arena is the area under the curve over the total possible 'volume' of the arena. The average instantaneous capture probability is:

$$\bar{p} = \frac{1}{A} \iint_A \frac{2}{e^{\lambda d_{x,y}} + e^{-\lambda d_{x,y}}} dx dy$$

This same approach can be extended for multiple traps; the sum of the volumes under the curves over the sum of the arena 'volume.' With many traps in close proximity, however, simple addition is problematic since it is possible to result in a larger numerator than the denominator and so an 'instantaneous' capture probability > 1 . Biologically, the addition also ignores trap interference (Suckling et al., 2015). It is helpful to consider the inverse of the capture probability, the escape probability $q (= 1 - p)$. This is because there is only one way to capture zero insects (none of the traps make a capture), but there may be many combinatorial possibilities of one or more captures. Given n traps each a distance $d_{x,y,t}$ from each trap t , we can calculate the average instantaneous escape probability as:

$$\bar{q} = \frac{1}{A} \iint_A \prod_{t=0}^n 1 - \frac{2}{e^{\lambda d_{x,y,t}} + e^{-\lambda d_{x,y,t}}} dx dy$$

One way to think about the instantaneous escape probability is that it represents the average probability of escape (=zero captures) if one were to randomly choose a location in the grid - equivalent to throwing a dart at a board. However, real insects in an invading population would have their positions correlated; there would be an incursion point and spread from that point. Furthermore, it is not clear how to move from the instantaneous capture probability to understanding the probability of capture over time as insects move around the area.

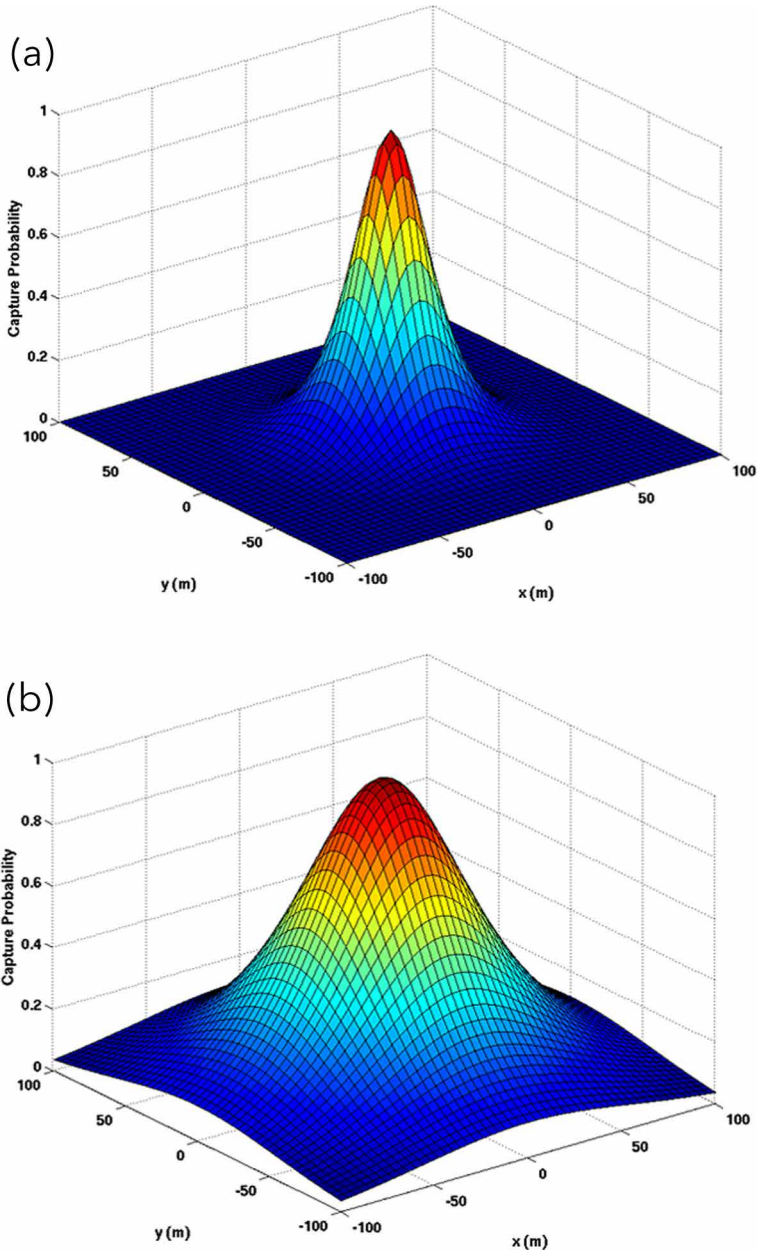


Figure 3 Three-dimensional representation of capture probability over (x,y) for two traps with varying attractiveness. (a) $1/\lambda = 15$ m and (b) $1/\lambda = 35$ m.

One of the simplest ways to model the dispersion of insects over space and time (T) is a diffusion model (Skellam, 1951; Kareiva, 1983):

$$\frac{dN(x,y,T)}{dt} = D \left[\frac{d^2N}{dx^2} + \frac{d^2N}{dy^2} \right]$$

Here N is the population density, time T is in days, D is the diffusion coefficient in m^2/day , and x, y are the positions in meters. The equation above yields a bivariate Gaussian (normal) distribution as a function of diffusion coefficient and T . For any given D , the variance of the bivariate normal will increase with time. The probability density function is:

$$g(x,y) = \frac{1}{2\pi\sigma^2} e^{-\frac{1}{2}\left(\frac{x^2+y^2}{\sigma^2}\right)}$$

Where σ is the standard deviation (we assume the mean position = 0) and can be calculated as $4\sqrt{DT}$. This also assumes standard deviations are equal in x and y dimensions and that there is no correlation in x and y positions. With these, we can calculate the distribution of individual insect positions each time step and then for each insect position calculate the probability of escape. TrapGrid, in its original release, returns the cumulative values of the means for each day over time, thereby estimating the average sensitivity of the grid over time in face of an invasive insect incursion at a given location.

The most recent release of TrapGrid includes an alternate calculation of capture probability: Strictly, the probability of capturing one or more insects. This measure is much more sensitive to the size of the population being modeled but may be useful in low-prevalence, small size trap grids. Full details are given in Manoukis and Hill (2021).

Another important feature of TrapGrid that will not be extensively discussed here is an alternate movement model besides simple diffusion: a random-correlated walk (Kareiva and Shigesada, 1983; Byers, 2001). This is more realistic in the sense that the positions of individual insects are correlated, rather than a new distribution of positions being generated at each time step as in the case of diffusion. It requires two parameters for movement (compared with one, D , in diffusion): mean step size and mean turning angle per time increment. For most insects, these are not available, but work is ongoing to measure these in the field for tephritid fruit flies (Miller et al., 2022).

2.2 Other models

Before discussing applications of TrapGrid, it is worth pausing here to note that TrapGrid and its underlying model are in no way the only attempt to

quantify trap network sensitivity. Here a few examples of other methods are provided to give a sense of the range of methods that have already been applied. Further, it is useful to understand other models when interpreting the results of field experiments performed to parameterize them (see Section 3.1).

The concept of trap attraction and insect capture has been represented in a variety of ways. One early idea was the 'Active Space' of Bossert and Wilson (1963), which focused on the distribution of a chemical signal over space modeled via a diffusion process, yielding a gradient in space over a variety of release conditions (still air, puffs of release, and more). Experimental applications of this model proved difficult, but the idea of modeling capture over space was clearly valuable (Nakamura and Kawasaki, 1977; Elkington and Carde, 1984).

Later work simplified the model of distance \times capture probability by introducing concepts like the 'sampling range,' 'range of stimulation,' and 'range of attraction' (Wall and Perry, 1987). These were defined, respectively, as the maximum distance from which an insect can reach a source over a given period, the maximum distance at which a behavioral response can be seen in a target insect, and the maximum distance at which insects can be shown to direct their movement toward the source. These are tangible measures that can be measured directly via experimentation, but their link to the application of trapping networks is less direct.

Byers et al. (1989) introduced a direct measure known as the 'effective attraction radius,' which they defined as the size of an unbaited trap that would be needed to have an equivalent capture as the trap with lure. In other words, what is the area within which there is a 100% probability of capture? This measure has a strong direct link to the application of traps, even though it was originally developed to estimate the densities of forest pests. Experimentally, it could be determined via the ratio of passive and baited trap catches. While the original formulation did not include insect movement, this was always possible and indeed was analyzed in subsequent studies (e.g. Byers, 1999).

Not all models of traps and insect captures include a function relating distance to probability of capture. A good example is the 'effective sampling area,' or ESA (Turchin and Odendaal, 1996). ESA is a conversion factor between the density of trappable insects and the number caught over a given period of time, and so tends to be used in situations where the goal is to estimate the population density (Puche and Su, 2004). It can be used to estimate the mean probability of detecting a randomly distributed insect in a trap network (Kean, 2015) and has been applied to questions outside of insects (e.g. crayfish, see Acosta and Perry, 2000). While a trap density for a minimum number of captures can be derived using the concept of the ESA, varying attraction of individual traps given environmental factors within a single grid cannot be as easily gauged or included.

Increasing computational power in the twenty-first century has opened new possibilities in trap network design, including improved models of insect movement, and indeed, its very consideration (Miller et al., 2015). Simulating time, movement, and lure plumes simultaneously is now possible with directly actionable results for agriculture (Adams et al., 2017). TrapGrid is an example of this sort of approach, geared to quantifying capture probability to support management decisions around how many traps to deploy and where. As demonstrated later, TrapGrid can be applied to a variety of situations.

TrapGrid has limitations. Like all models, it does not consider all relevant factors, but only a selected subset and those that it does consider are simplified for mathematical representation and tractability. Some of the biological factors currently not modeled by TrapGrid include the receptiveness of a given insect to the lure being used in the trap network, the efficiency of the trap at capturing an insect that enters, or any consideration of a demographic change in the target insect population. Furthermore, the exiting implementation provides only trap-network-wide results rather than the probability of capture in given traps. Finally, TrapGrid requires an attraction parameter that must be estimated via field studies for given insect-trap/lure combinations, and only a limited number of these have been developed to date.

3 Applications

3.1 Estimating trap attraction

The question of how far an attractant-baited trap can draw its captures has been extensively investigated by entomologists for many different species (see Schlyter, 1992). Perhaps the most common approach has been via Mark-Release-Recapture (MRR) experiments with a centrally located trap and releases at varying distances (e.g. Dodds and Ross, 2002; Shelly et al., 2010; Shelly, 2021). While these experiments clearly provide very useful information, recaptures for a given distance often have high variance and there is difficulty setting sufficient release points at increasing distances since the area under consideration increases rapidly (and with it, increasing variation). As an example of the limitations of this sort of study, it has been noted that estimates of dispersal for given species seem to be highly related to the size of the trapping grid employed in the particular study (Weldon et al., 2014).

There have been novel efforts to improve this situation. A relatively recent study cleverly leveraged the ability to turn blacklight traps on and off to estimate both the range of attraction and spatial interference against *Culicoides* midges (Rigot and Gilbert, 2012). In an example using chemical lures, Jactel et al. (2019) offered a method based on pairs of traps, at varying distances apart, monitoring wild populations of *Monochamus galloprovincialis*

(pine sawyer beetle), and leveraging trap interference to estimate the attractive range of sex pheromone-baited cross vein traps. They reported higher attractiveness at distance than previous MRR- based studies, but the comparison was indirect due to different measures of trap attraction used in the various studies (Section 2.2). The utility and applicability of field results are highest when the experiments are linked at the time of design to mathematical models of trapping (Dufourd et al., 2013).

To date, only two studies have been published with results of field experiments designed specifically to estimate λ (Manoukis and Gayle, 2015; Manoukis et al., 2015), and they illustrate the interplay between field experiments and underlying mathematical models. Both were MRR experiments in a grid of traps, where the proportion of released insects recaptured (P) was used to infer the λ value that would result in the observed P .

Manoukis et al. (2015) marked and released both Mediterranean fruit fly ('Medfly') and the Oriental fruit fly ('OFF'; *Bactrocera dorsalis*) in three spacings (50 m, 100 m, and 150 m) of 8×8 grids of Jackson traps baited with male lures (trimedlure and methyl eugenol, respectively). Experiments were completed in two environments, a macadamia orchard on the east side of Hawaii island and a pahoehoe lava field on the west side. Results are given in Table 1.

Focusing on the first set of results (rows 1–3 in Table 1), a relatively high P value is evident for OFF in macadamia in a grid with 150 m spacing in x and y directions (mean = 0.623). Using TrapGrid (see section 2.1), the relationship between trap attraction and P is plotted for an 8×8 grid of traps with 150 m spacing. The P value of around 0.62 in a 150 m grid translates to a $1/\lambda$ over just over 40 m. A second line is plotted for the same relationship, but this time in a grid that has 75 m spacing. From this line, the expected recapture should be between 0.95 and 0.99 in the 75 m grid based on the $1/\lambda$ value of ~40 m, from the results in the 150 m grid (Fig. 4). This is an extremely high bar in MRR studies, but the subsequent three rows in the table show that there was a good match to the theoretical expectation. In overall experiments, in both environments, the $1/\lambda$ for methyl eugenol was estimated to be around 36 m for receptive OFF males.

Continuing down Table 1, methyl eugenol is confirmed to be a more effective lure for male OFF than trimedlure is for Medfly, and it is more consistent across environments (for Medfly $1/\lambda$ approximately 14 m in macadamia, about 7 m in the lava field). While the environment difference in λ between lava field and macadamia orchard for Medfly has some caveats, it does suggest that models of insect traps should include variable attraction for a given lure-target species combination (Manoukis et al., 2015). Further experiments with other tephritid species are needed, and besides the labor and difficulties of MRR experiments, there is no reason similar experiments could not be conducted to estimate $1/\lambda$ for other insect species.

Table 1 Results of Mark-Release-Recapture experiment by Manoukis et al. (2015) on Hawaii Island. Three grid spacings, in two environments, are reported for two species *Bactrocera dorsalis* (OFF) and *Ceratitidis capitata* (Medfly). The proportion of each release cohort responsive to the lure ('Res.') was assessed at the time of the experiment via Y-tube olfactometer assay; this proportion times the estimated number released ('Rel. '), gives the number of available for recapture (denominator of the P calculation, not shown). The number recaptured ('Rec.') is the numerator.

| Date | Habitat | Spacing (m) | Species | Rel. | Rec. | Res. | P | 1/λ |
|------------|-----------|-------------|---------|------|------|------|-------|-------|
| 2013-07-08 | Macadamia | 150 | OFF | 1256 | 375 | 0.58 | 0.519 | 34.94 |
| 2013-07-10 | Macadamia | 150 | OFF | 2011 | 783 | 0.60 | 0.649 | 41.49 |
| 2013-07-12 | Macadamia | 150 | OFF | 1987 | 1256 | 0.90 | 0.702 | 44.58 |
| 2013-07-22 | Macadamia | 75 | OFF | 1890 | 1192 | 0.70 | 0.904 | 31.59 |
| 2013-07-24 | Macadamia | 75 | OFF | 2117 | 1557 | 0.88 | 0.841 | 28.15 |
| 2013-07-26 | Macadamia | 75 | OFF | 2062 | 1824 | 0.93 | 0.956 | 37.75 |
| 2013-08-19 | Macadamia | 150 | Medfly | 1786 | 102 | 0.55 | 0.104 | 14.46 |
| 2013-08-21 | Macadamia | 150 | Medfly | 1716 | 105 | 0.55 | 0.112 | 15.08 |
| 2013-08-23 | Macadamia | 150 | Medfly | 1581 | 126 | 0.45 | 0.177 | 18.9 |
| 2013-09-02 | Macadamia | 75 | Medfly | 1372 | 312 | 0.61 | 0.374 | 14.20 |
| 2013-09-04 | Macadamia | 75 | Medfly | 1956 | 336 | 0.57 | 0.301 | 12.45 |
| 2013-09-06 | Macadamia | 75 | Medfly | 2034 | 275 | 0.56 | 0.243 | 10.97 |
| 2013-09-23 | Lava | 100 | OFF | 1778 | 564 | 0.43 | 0.746 | 31.70 |
| 2013-09-25 | Lava | 100 | OFF | 1907 | 457 | 0.28 | 0.871 | 38.87 |
| 2014-01-15 | Lava | 100 | Medfly | 1443 | 47 | 0.39 | 0.084 | 8.25 |
| 2014-01-17 | Lava | 100 | Medfly | 1778 | 38 | 0.60 | 0.036 | 5.65 |

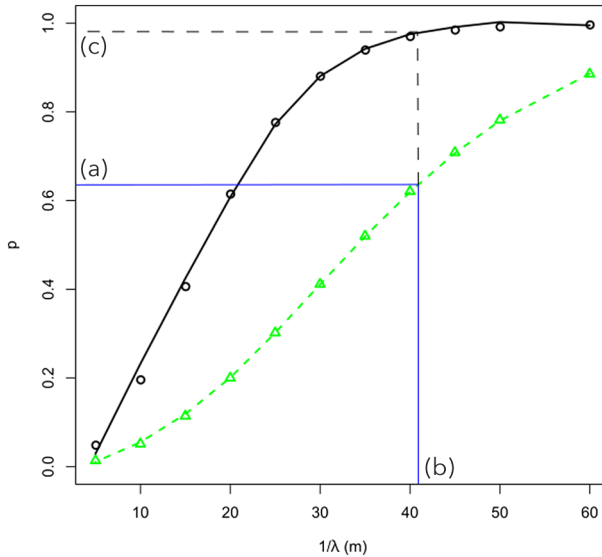


Figure 4 Expected proportion recapture (P) in a 75 m grid (black line, circles) based on attraction ($1/\lambda$) inferred for a 150 m grid (green broken line, triangles). The P for the 150 m grid in the first experiments was around 0.62 (a); this corresponds to $1/\lambda$ of about 40 m (solid blue line, point b). This attraction would yield a recapture rate of about 0.97 for the 75 m grid (broken line, point c). The observed average P for the 75 m grid in subsequent experiments averaged 0.90; close to expectation (Table 1).

3.2 Large area surveillance

As mentioned in section 1, tephritid fruit flies are some of the most economically important agricultural pests in the world. They are noted for their highly invasive characteristics (Duyck et al., 2004). Some species, such as Medfly and OFF are capable of laying eggs in the fruit of hundreds of hosts, estimated at 419 and 500 plant species and varieties, respectively, with many of commercial interest (Liquido et al., 2020, 2021). After eclosion, the larvae of these fruit flies consume the fruit, making it unsuitable for the market and introducing rotting and spoilage. Third instar larvae leave the fruit to pupate in the soil, finally emerging as adults to begin the life cycle again (Vargas, 1989). Because of their economic impact, many tephritids are considered quarantine pests, and their introduction to new areas can lead to loss of market access in addition to the direct damage (Kruger, 2016).

Fruit fly establishment in production areas thus carries a large potential economic cost. For this reason, surveillance networks are employed around the world (see section 1). An important question arising is: How many traps should be deployed, and in what configuration, to attain an acceptable level of surveillance sensitivity? Many trap networks are designed and deployed without any ability or attempt to quantify capture probability, rather than relying

on expert opinion and extrapolation. TrapGrid was originally developed to provide quantitative results addressing this question.

An example can be useful to understand how TrapGrid can be used. The California Department of Food and Agriculture has a well-documented approach to surveillance against fruit flies (Gilbert et al., 2013). For OFF in Southern California, this includes five methyl eugenol-baited Jackson traps per square mile over almost all the greater Los Angeles area plus five torula yeast-baited McPhail traps. A sample grid of the methyl eugenol traps only is shown in Fig. 5a over an area equivalent to Orange County, California. This grid consists of a total of 6738 traps, indicating the effort and cost associated with surveillance trapping in a single county.

Could this or a similar number of traps be deployed more efficiently than a uniform density across a wide area? Incursions of OFF are found several times per year in Southern California, so improvements could have a significant impact on the biosecurity of the State. One very simple approach would be to increase the density of traps in areas with a higher probability of OFF detection based on previous years while decreasing the density in areas where historically not as many OFF have been found. Fig. 5b gives a modified trap network comprising fewer traps (5643) but with variable density: three traps per square mile in areas with fewer detections, and six traps per square mile in areas with higher levels of detection.

TrapGrid can be used to quantify the average capture probability of each of these grids and enable direct comparison. Using the model with simple diffusion and the outbreak locations shown in Fig. 5b, the uniform grid in Fig. 5a has a mean capture probability after 30 days of 0.130 (range: 0.054–0.183). The variable grid in Fig. 5b yields an average capture probability of 0.115 (range: 0.033–0.187). These are comparable sensitivities, with a drop of almost 1100 in the number of traps deployed.

The realism of the results from the TrapGrid model will depend heavily on the quality of the information available on past outbreaks. Additionally, estimates of attraction are critical (Section 3.1). It is also important to have estimates of the diffusion of the pest, a question that has recently been addressed using real-world surveillance data (Caton et al., 2021b). It is also possible that the map of outbreak risk could change over time, so it might be important to redeploy a uniform grid for a few years in line with predicted and observed environmental change to re-assess which areas should be trapped at high and low densities. Despite these issues, this example gives an idea of the potential to improve surveillance efficiency and sensitivity by quantifying capture probability.

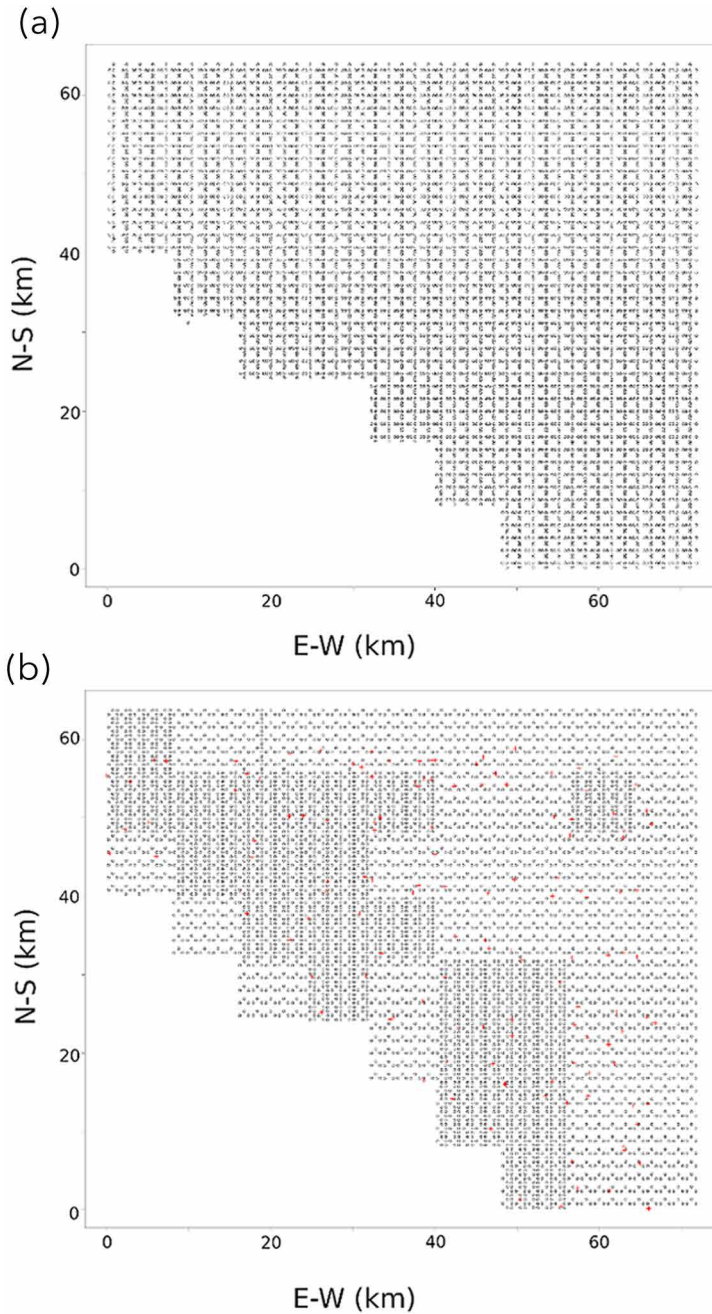


Figure 5 Hypothetical uniform (a) and varying (b) density distribution of traps over Orange County, California. In (b), the red 'x' symbols indicate hypothetical locations of detections that would guide the application of a variable density.

3.3 Other applications

The example in Section 3.2 is at the heart of the original goal for TrapGrid: Landscape-level average trap network sensitivity estimation over time to allow comparison of alternative trap layouts. However, in the time since the model was released, it has been used for other applications. One of these has been to evaluate delimitation grids, as mentioned earlier (Caton et al., 2021a). These same authors employed TrapGrid to vary diffusion coefficients to estimate the dispersal ability of a variety of invasive pests based on surveillance trapping grid data (Caton et al., 2021b).

Low-prevalence situations at a smaller scale, e.g. individual orchards, are also in the process of being examined and quantified via TrapGrid (Manoukis and Hill, 2021). In this context, the goal is to evaluate the potential demographic meaning of a given number of captures across a small trap network - a monitoring situation. Estimating the standing population size of an endemic pest insect can be helpful for systems approaches used to ensure phytosanitary exports and general biosecurity - a low starting population size is regularly an important component of these approaches (Ruesink, 1976; Quinlan et al., 2020).

TrapGrid could also be used to ask questions about how many traps over what area might be needed to create a barrier that traps effectively all insects attempting to cross. Such an application would require a new implementation of the model or significant modification of the existing code since the current version does not track or return information on which traps captured which insects (Manoukis, 2020). Individual-based tracking via a random-correlated walk model would also be critical for this application.

The MRR experiments described in Section 3.1 point to another useful application of TrapGrid: Estimating and comparing trap attraction. In addition to the question of comparing lures between species and in different environments, attraction to wild and colony-reared insects has been examined (Manoukis and Gayle, 2015). Other possible biological questions that could be tested include the effect of lure age, various formulations, the presence or absence of host trees, insect age, etc. Future development of TrapGrid could also include the ability to include habitat maps/geographic information system layers to more realistically represent the environment of the insect and its effect on movement and capture probability.

4 Practicum

In this section, a step-by-step example of the application of TrapGrid is presented as a guide for those interested in using the model. An overview of necessary steps and some starting points for executing each for their own systems are given first.

To illustrate a simple case, let us assume a user wanted to compare the instantaneous capture probability as well as the average cumulative capture probability after 30 days of a single square kilometer with 12 evenly spaced, low attraction traps ($1/\lambda = 8$ m) plus 4 or 16 highly attractive traps ($1/\lambda = 30$ m). The goal of the trapping might be for monitoring, and the user is trying to determine if the additional traps are worth the added cost of materials and servicing, especially since the more attractive traps (pheromone baited) are more costly than the less attractive ones (these are food-based).

The first step is to define the (x,y) positions of each trap, as well as the total grid. This can easily be done in Excel (Microsoft Corp., Redmond, WA, USA) or similar spreadsheet software. A sample plot from such a spreadsheet is shown in Fig. 6. Positions in the columns for the plot can be changed dynamically to test different layouts.

Two sets of points are saved as 'tab separated value' files: One with the 12 low attraction traps plus 4 high-attraction traps indicated by orange 'X' symbols in Fig. 6, and the other with the 12 low attraction traps plus all 16 ('X' and '+' symbols) high-attraction trap points. The first of these is shown in Box 1 as a sample.

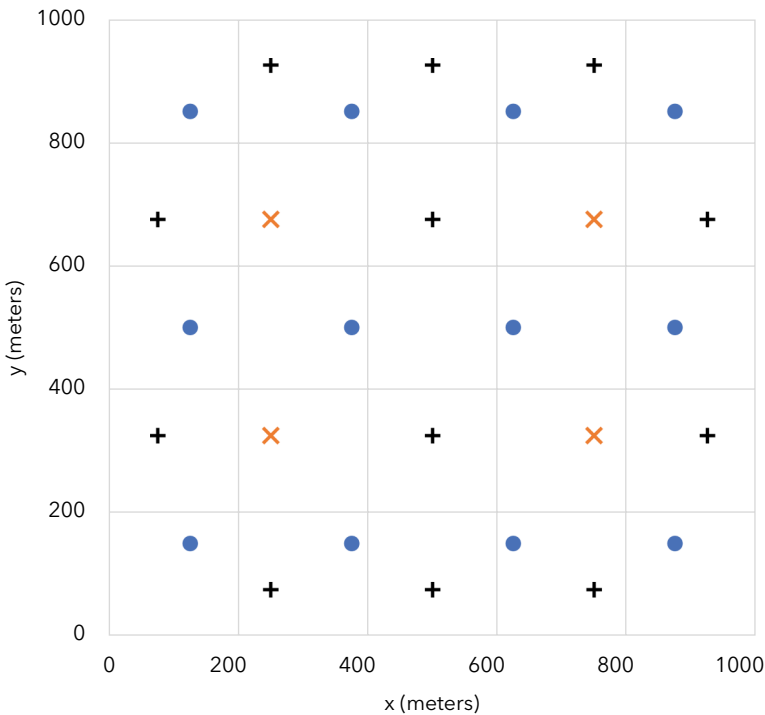


Figure 6 Trap positions in a 1 km^2 area for a test of instantaneous and cumulative average capture probability. Blue dots are low attraction traps ($n = 12$; $1/\lambda = 8$ m). Orange 'X' points are high-attraction traps ($n = 4$; $1/\lambda = 30$ m). Black cross points are additional high-attraction traps ($n = 12$, 16 when combined with 'X' points; $1/\lambda = 30$ m).

Box 1 Sample TrapGrid file, tab-separated-values (*.tsv). First line is grid dimension in x and y. Each subsequent line represents a trap, first value is x, second is y, and third is $1/\lambda$ (attraction).

```
1000 1000
125 150 0.125
375 150 0.125
625 150 0.125
875 150 0.125
125 500 0.125
375 500 0.125
625 500 0.125
875 500 0.125
125 850 0.125
375 850 0.125
625 850 0.125
875 850 0.125
250 325 0.033
750 325 0.033
250 675 0.033
750 675 0.033
```

When creating TrapGrid files, it is important to ensure that there are no invisible characters as these may interfere with parsing by the TrapGrid program. For example, an extra tab after the second dimension on line 1 (inserted by default by most spreadsheet programs) will cause a parsing error. So will an additional line break at the end of the file, or additional tabs after an attraction value. It is best to verify these files in a text editor that can display non-printing characters. Use of a word processor such as Microsoft Word is highly discouraged, as this will likely introduce formatting, spellcheck, etc.

With the trap grids defined, the next step includes running the TrapGrid program, freely available online at <https://github.com/manoukis/TrapGrid>. The program is written in Java and should be executable on any major operating system including Microsoft Windows, Apple MacOS (Apple Corp., Cupertino, CA, USA), or variants of Linux. TrapGrid is run from the command line; help is available by entering the following command in the directory containing the program:

```
java -jar TrapGrid.jar --help
```

To run our first set of simulations, assuming the TrapGrid file (named 'tg16traps.tsv,' contents of which are in Box 1) and the program executable are in the same directory, we use the following command:

```
java -jar TrapGrid.jar -tg tg16traps.tsv -nd 30 -ns 100 -nf 150 -dc 5000 -s 25361 --calculateAvgEscProb > tg16traps-output.txt
```

The first three terms of the command invoke the program by having the system-installed Java Virtual Machine execute the 'jar' file containing the program. After the '-tg' switch, the TrapGrid file is passed to the program. -nd indicates the number of days over which to run the simulations (30), -ns is the total number of simulations to run (100), -nf is the number of flies per simulation (150), -dc is the diffusion coefficient D (5000 m²/day), and -s is a random seed (optional, but useful for repeatable results; set to 25 361, can be any integer). The next switch '--calculateAvgEscProb' sets the program to calculate the instantaneous escape (capture) probability. Finally, the '>' operator and file name allow the terminal program to redirect the output to a text file for later viewing (file will be named 'tg16traps-output.txt'). The same command as mentioned earlier can be reused but changing the trap file from tg16traps.tsv to a different one with 28 trap lines specified which include the additional high-attraction traps. A different output file is also recommended.

Program execution for these grids took less than a minute on a current commodity portable machine (Intel Core i5-1145G7 @ 2.6 GHz, 16 GB RAM). Larger grids, more simulations, or more traps can increase this execution time significantly, especially if the instantaneous escape probability is calculated. In those instances, more computing resources or time will be required.

The output file will include a block at the top with parameters, program version information, and the instantaneous escape probability. An average cumulative escape probability is then given for each of the 30 days of the simulation - this average is across all 100 simulations. The individual 100 simulation cumulative escape probabilities are then given later. As noted earlier, capture probability P is simply $1 - q$ (where q is the escape probability).

The 16-trap grid has a higher instantaneous escape probability (0.949) compared with the 28-trap grid (0.831) as expected. These values reflect the probability that a point selected at random from anywhere in the 1 km² grid yields a capture. Over time, the 28-trap grid also performs better in terms of cumulative capture probability (Table 2). While qualitatively unsurprising, the difference might be - 16 traps have an average cumulative capture probability after 30 days of under 60%, but with the addition of the extra high-attraction traps the value increases to over 93%. Depending on the cost of the traps, goals of the program, and required accuracy in monitoring, the additional traps may be worth the cost.

While the example mentioned earlier is very simple, it illustrates many of the important functions of TrapGrid. One of the additional capabilities worth mentioning is the ability to define population starting points ('outbreaks' in the case of surveillance) via an 'outbreak file.' This is a two-column, tab-delimited file

Table 2 Capture probabilities over time for the 16- and 28-trap grids; initial outbreak positions random for each of the 100 simulations per grid.

| Day | 16-Trap grid | 28-Trap grid |
|-----|--------------|--------------|
| 1 | 0.048 | 0.156 |
| 2 | 0.090 | 0.273 |
| 3 | 0.129 | 0.368 |
| 4 | 0.163 | 0.445 |
| 5 | 0.195 | 0.509 |
| 6 | 0.224 | 0.564 |
| 7 | 0.250 | 0.610 |
| 8 | 0.275 | 0.649 |
| 9 | 0.299 | 0.683 |
| 10 | 0.321 | 0.713 |
| 11 | 0.342 | 0.739 |
| 12 | 0.362 | 0.762 |
| 13 | 0.379 | 0.782 |
| 14 | 0.396 | 0.800 |
| 15 | 0.412 | 0.816 |
| 16 | 0.427 | 0.831 |
| 17 | 0.441 | 0.843 |
| 18 | 0.454 | 0.854 |
| 19 | 0.467 | 0.865 |
| 20 | 0.479 | 0.874 |
| 21 | 0.491 | 0.883 |
| 22 | 0.501 | 0.891 |
| 23 | 0.512 | 0.898 |
| 24 | 0.522 | 0.904 |
| 25 | 0.532 | 0.910 |
| 26 | 0.541 | 0.916 |
| 27 | 0.550 | 0.920 |
| 28 | 0.558 | 0.925 |
| 29 | 0.565 | 0.929 |
| 30 | 0.573 | 0.933 |

with each row containing an x and y position, in meters, from which populations are simulated. If this file is specified via the '-ob' switch at the command line, then TrapGrid will only run as many simulations as there are lines in the file. The ability to define population locations is often important for real-world simulations (e.g. MRR experiments with a defined release point in a trap grid).

Finally, a note on transforming latitude/longitude data into x,y positions in meters. There are many ways to accomplish this task, but a simple one that is usually sufficient for most grid sizes is to define an origin point and then convert each of the trap positions by using the number of meters per degree latitude and longitude for the study area. Using the WGS84 spheroid this can be approximated for latitude via:

$$M_{d,t}(\phi) = 111132.92 - (559.82 * \cos(\phi)) + (1.175 * \cos(4\phi)) \\ + (0.0023 * \cos(6\phi))$$

The equivalent equation for longitude is:

$$M_{d,g}(\phi) = ABS(111412.84 * \cos(\phi)) - (93.5 * \cos(3\phi)) \\ + (0.118 * \cos(5\phi))$$

The difference in each dimension between the origin point and each trap can be calculated in degrees and converted to meters. The origin, trap, or midway point of latitude can be used for ϕ , results will be very similar for most grid sizes.

5 Conclusion

In this chapter, a high-level overview of the goals of trap networks, some examples and details for tephritid fruit flies, and then a detailed description of the TrapGrid model are given. TrapGrid can be used to quantify the probability of capturing insects instantaneously or over time using a function that relates distance from a given trap to the probability of capture and two models of insect dispersal. Brief descriptions of other modeling approaches to these questions, some of which have seen application outside of research, are discussed followed by ideas for the application of TrapGrid, including a way to determine trap attraction (the parameter λ in the model) and how to compare alternative trap layouts on a landscape scale. Finally, in the practicum, a working example was given comparing two alternative trap layouts in a 1 km² area via quantification of capture probability instantaneously and over 30 days. There remain other, undescribed, applications of TrapGrid and similar models to improve insect pest monitoring, surveillance, and control. This chapter serves as a useful starting point for researchers and practitioners interested in potential applications which optimize trapping surveillance and control of pest insects. A version of TrapGrid that includes the features described here is available at <https://github.com/manoukis/TrapGrid>.

6 Where to look for further information

There are a number of comprehensive sources on trapping and its application. A relatively recent book edited by Shelly et al. (2014) is very helpful for those interested in trapping of fruit flies from biology, to ecology, to programs and application. From a theoretical perspective, the book by Miller et al. (2015) provides a very helpful framework to consider insect trapping in a concise and readable presentation. Muirhead-Thompson's (1991) work is also an excellent resource on trapping across a wide variety of insects.

From the program and regulatory perspective, the regional plant protection organizations as defined by the International Plant Protection Convention of 1997 (https://nappo.org/application/files/5515/8319/2828/IPPC_new_revised_text.pdf) are helpful to follow. Examples include the North American Plant Protection Organization (NAPPO; <https://www.nappo.org/>) and the Asia and Pacific Plant Protection Commission (APPPC; <https://www.fao.org/asiapacific/apppc/en/>). A full list of the 10 regional plant protection organizations is available at <https://www.ippc.int/en/external-cooperation/regional-plant-protection-organizations/>.

The International Atomic Energy Agency and the Food and Agriculture Organization maintain multiple online resources that are useful, especially for those focused on Tephritids. These include the TWD (Tephritid Workers Database) and 'Fruit Fly News'. Trapping comes up regularly in the context of SIT programs. Links to these are available at <https://www.iaea.org/resources/nucleus-information-resources> and <https://nucleus.iaea.org/sites/naipc/twd/Newsletters/Forms/Fruit%20Fly%20News1.aspx>.

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