Use of Semiochemicals for Survey and Detection of Exotic Insects: Principles and Constraints

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Abstract

This review concentrates on the principles of surveying for exotic invaders with semiochemical-baited traps and examines three possible strategies for improving detection of exotic insects. 1) What constrains the development of traps having an extended range of attraction? 2) Is the trap's detection sensitivity influenced by the failure of some insects attracted to a trap to be captured? 3) What empirical and simulation techniques can be used to enhance our understanding of the meaning zero trap catch and to optimize spatial patterns of deployment? Selected evidence from a variety of survey and detection cases is considered, but examples relate mainly to survey methods used to detect the spread and invasion of the gypsy moth (*Lymantria dispar*), which is a species of special interest. It is concluded that improvements in the technology of trapping are attainable with simple behavioral assays. Such improvements should lower the cost of surveys and enhance their reliability. Correlation of negative trap catch with the probability of missing an incipient infestation remains at the heart of survey interpretation. Mark-recapture protocols and simulation modeling are two techniques that should prove useful for improving patterns of trap deployment and interpretation of survey results

Introduction

Semiochemical-baited traps are widely used for monitoring of insect movement and detection of invasive species. Such traps release odorants mediating flight towards a wide variety of resources, including attraction to a mate, to sources of adult food, or to an oviposition site. Many kinds of survey traps are baited with sex-attractant pheromones; when pheromone-baited traps are deployed in a grid, they often are capable of detecting populations at very low density. Traps baited with lures based on odors used in detecting adult food also have proven crucial to some survey programs that attempt to detect a spectrum of true fruit fly species with a single type of trap. Other monitoring programs for tree-infesting beetles have relied on traps baited with host odor such as alpha-pinene or ethanol. Such non-specific lures may sample insect populations only in the immediate vicinity of the trap. In a few cases, the behavioral and ecological *raison d'être* for attraction to a compound remains enigmatic. For example, for 85 years male Mediterranean fruit flies, *Ceratitis capitata*, have been known to be attracted to methyleugenol (called "medlure"). One possible explanation for the attractive properties of medlure and the related compound trimedlure is that both stimulate aggregation (lekking) behavior of males as a prelude to attraction of females and mating. These two compounds, however, are not released by males, nor do they seem to be released by plants on which natural aggregations occur in the field (Cunningham, 1989). There are also many trapping systems based on insect attraction to traps that mimic only the visual features of a resource. For example, the attraction of many phytophagous insects to yellow panels (typically with a peak reflectance of light near 550 nm) relies on this hue mimicking the peak wavelength of reflectance from green leaves. These selected examples illustrate that trap-based survey and detection programs rely on a spectrum of insect responses to resources.

The probability of detecting of an incipient population is highly correlated to the density of traps, and the cost of deploying a survey grid rises with density of traps set out. There would appear to be two seemingly straightforward ways to improve the sensitivity of survey traps: first, enhance the "range" of a trap by luring insects over greater distances, or, second, capture a greater proportion of insects arriving at the immediate vicinity of the trap. Regardless of the traps' range and efficiency of capture, interpretation of trap catch is a fundamental problem. For example, interpretation of zero catch in a grid of survey traps remains problematic: What is the probability that the survey has failed to detect a population? Conversely, when one or more adults are recovered from a trap, it can be difficult to determine from where the trapped individuals originate.

This review will emphasize the principles of surveying for exotic invaders with semiochemical-baited traps and examine three possible strategies for improving detection of exotic insects. First, what constrains the development of traps having an extended range of attraction? Second, is the trap's detection sensitivity influenced by the failure of some insects attracted to a trap to be captured? These two issues are related to how a plume of semiochemical diffuses in wind and how the target insect reacts to this dispersion pattern and instantaneous wind direction. A third consideration is what empirical and simulation techniques can be used to enhance our understanding of the meaning zero trap catch and to optimize spatial patterns of deployment?

To explore these issues, selected evidence from a variety of survey and detection cases will be considered, but a principal example will be survey methods to detect the spread and invasion of the gypsy moth (*Lymantria dispar*). This species is of special interest because established populations, now ranging from throughout the northeastern United States south to the Carolinas and to the upper Midwest, have the potential to invade much of the remaining United States, and there is an active management program (STS or Slow the Spread) to retard its range expansion. Also, there is an occasional introduction of the Asian strain of the gypsy moth, usually to the west coast of North America via commercial shipping from the Russian Far East. The Asian strain is of special concern because, unlike its established North American counterpart, the female is capable of flight, and, therefore, the potential for rapid range expansion is greater than with the North America strain. Gypsy moth invasion is detected by capture of males in traps baited with (+)-disparlure, the female-emitted pheromone. The number of gypsy moth traps deployed in the United States by state agencies in cooperation with APHIS and the Forest Service is remarkable: 300,000 to 350,000 yearly. The cost to procure, set and retrieve an individual survey trap varies with the density of placement, terrain, and to some extent how an agency calculates costs: cost per trap ranged between $18 and $80. In 2000, APHIS estimated the expenses for monitoring of the Asian and European strains at $5,735,671. The cost of traps used in the Slow the Spread (STS) Program was $4,490,000, for a combined total of $10,225,671 (V.C. Mastro, personal communication).

Meteorological and Behavioral Factors Influencing Trapping Range

Patterns of pheromone dispersion. Turbulent diffusion is the dominant process influencing the structure of odor plumes as they are transported downwind (Murlis et al., 1992). Molecular diffusion in contrast has relatively little effect on the plume dispersion because its scale of movement (ca. 2 mm s^{-1}) is comparatively small. Turbulence causes an initially small emission of odorant to expand into a plume comprised of odor filaments interspersed with pockets of "clean" air (Figure 1). When an odor is sampled at a fixed position downwind, it appears as a series of bursts interspersed with gaps of "clean" air (Murlis et al., 2000). When the signal is present, it fluctuates continually in intensity. The absence of the signal over large fractions of a second or longer intervals of time becomes more prevalent as the distance away from the odorant source increases. As the plume is carried downwind and expands, the average concentration of odor within the plume's boundaries declines. Moment-to-moment contact with individual filaments of odorant seems to govern the insect's upwind heading and velocity, at least among moths (Mafra-Neto & Cardé, 1994; Vickers & Baker, 1994).

Many meters away from the odor's source, some filaments still harbor relatively high concentrations of odor, suggesting that insects should detect odorant

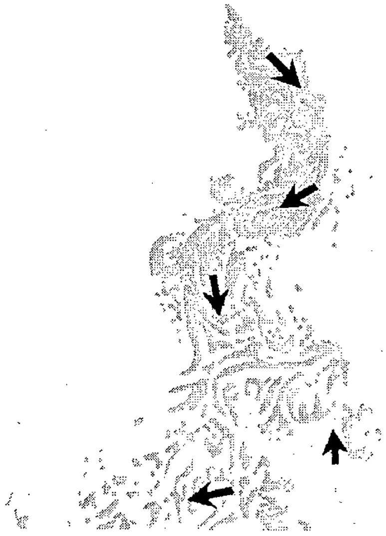

Figure 1. View from above of a 2-D representation of the instantaneous, above-threshold concentration of semiochemical from a point source dispersed in wind. The plume's origin is from the top and the plume's meandering path is caused by changes in the wind's velocity and direction. The arrows indicate instantaneous wind direction. An organism attempting to locate the source of the odorant by flying upwind while within the plume frequently would encounter gaps of "clean" air and an upwind trajectory often would take the responder beyond the plume's boundaries.

from a trap at substantial distances downwind. Experimental evidence for such behavioral capabilities in insects is limited but persuasive. Individually caged male gypsy moths show by a wing-fanning response that they can readily detect a plume of synthetic pheromone in a forest at least 120 m downwind of its source (Elkinton et al., 1987). Presence of an odorant in an above-threshold concentration, however, does not signify that there is sufficient information available for a male moth to routinely navigate a course to the plume's origin. When gypsy moth males detecting pheromone (as evidenced by wing fanning) were released at distances up to 120 m downwind of the pheromone source, fewer than 10% of the males eventually reached the pheromone source (Elkinton et al., 1987). Those males that located the source did so with a mean transit time of 9 minutes. Had their flight been continuous and directly along the plume, males should have reached the source within several minutes, given their observed average net velocity of ca. 0.5 m s^{-1} flying along pheromone plumes in the field (Willis et al., 1994). The first problem is that turbulence causes the plume to be discontinuous (Figure 1), with the consequence that a male flying along the plume will encounter patches within the plume where pheromone is not detected. If the gap in the detection of odor is about a second or longer, progress toward the source ceases (Kuenen & Cardé, 1994). The second issue is that changes in wind direction and velocity cause the plume to meander, with the instantaneous direction upwind being aligned only infrequently with the plume's long axis (Figure 1) (Elkinton et al., 1987; Brady et al., 1989).

Orientation to plumes from distant odor sources. Progress upwind with the plume is mediated by optomotor anemotaxis (reviews: Baker 1990; Arbas et al., 1993; Cardé, 1996). The only mechanism by which airborne organisms can detect the direction of wind flow while airborne is to apprise visually how wind has altered their flight path. In brief, this mechanism uses the flow of the insect's visual surround to determine its direction of movement with respect to the wind. If the flow of the visual field beneath the insect is front-to-back, then the insect is aligned with the wind. Upwind- versus downwind direction could be set by comparing the rate of its perception of longitudinal flow and either thrust or mechanosensory information. If the flow of the visual field has a transverse (to-the-side) component, then the insect can gauge that its trajectory is not directly upwind and redirect its course. Optomotor anemotaxis has been verified experimentally using wind tunnel assays in several moth families and in *Drosophila* flies (David, 1982) and *Aedes* mosquitoes (Kennedy, 1940).

A second mechanism to achieve upwind displacement is "aim-and-shoot." In this maneuver, the insect simply uses mechanoreceptors to detect the upwind direction before take-off. The direction of the ensuing flight path is maintained by following a visual course aimed towards the previously sensed upwind direction. If contact with odor is lost, then landing ensues; if odorant is encountered again, flight resumes. Because of the plume's fragmented nature and discontinuities between the wind direction and the plume's long axis, progress towards the odor source over distances of many meters would occur as a series of "steps" of intermittent flights and landings. Evidence for the aim-and-shoot maneuver comes mainly from onion maggot flies (Dindonis & Miller, 1980), cabbage root flies (Finch & Skinner, 1982) and tsetse flies (Bursell, 1987; Brady et al., 1990). It is important to recognize that many, if not all, of the insects employing the aim-and-shoot maneuver may switch while in flight to conventional optomotor anemotaxis. The optomotor reaction might be engaged either when wind is of sufficient magnitude to supply unambiguous directional information, or when the course set by aim-and-shoot maneuver and the upwind direction gauged by the optomotor response are in conflict. The precise wind velocities influencing the presumed shuttle between these two maneuvers remain to be determined, but such a redundancy in orientation strategies would seem to be an advantageous way to cope with either wind speeds or light levels that might be insufficient for the optomotor reaction.

Significance of plume structure and orientation mechanisms to the effective range of a semiochemical lure. Because of the fragmented distribution of odor within the plume, an insect heading upwind within the plume's boundaries frequently will encounter patches of odorant-free air, especially well downwind of the odorant's source where signal intermittency is high (Figure 1). When such gaps in odorant are encountered, upwind movement ceases. Further progress toward the source of the odorant requires a strategy for re-contacting the odorant. An insect may either "cast" (side-to-side-sweeps without upwind progress) (Keuenen & Cardé, 1994) or loop downwind (Kerguelen & Cardé, 1997). If the odorant is re-contacted, then upwind flight can resume. The frequent misalignment of the upwind direction with the plume's long axis (Figure 1) means that an insect flying upwind within the odor plume often will exit the plume, but the strategies of casting or looping will facilitate plume re-entry.

The plume's patchy internal structure and the misalignment of the instantaneous wind direction with the plume's long axis both dictate that gypsy moth males could not routinely (or quickly) navigate a course to a pheromone source located quite some distance upwind, despite their ability to detect the presence of the pheromone (Elkinton et al., 1987). Female gypsy moths, communicating their availability and their upwind location by release of pheromone, face the same meteorological constraints to extending of their distance of communication as those that limit the range of pheromone-baited traps. Increasing the rate of pheromone release will not appreciably increase the probability of females or traps luring a moth, even though the detectable threshold will extend farther downwind. (A parallel situation exists for males; males that are more sensitive to pheromone – that is those having a lower threshold of response – would be able to detect a plume at increased distances away from the female, but their ability to find the female would remain constrained by the characteristics of a patchy plume and the misalignment of wind direction and the plume's long axis.) The limitations of plume fragmentation and instantaneous wind direction are applicable to all organisms orienting upwind to point sources of odorant. Therefore, attempts to devise detection traps that are more sensitive by increasing the rate of lure emission face meteorological limitations.

Meteorological and Behavioral Factors Influencing Capture in Traps

Measuring efficiency of trap capture. Leaving aside the issues of long-distance orientation, what is the probability of an insect being captured after it has arrived at the vicinity of the trap? There are relatively few quantitative studies bearing on this issue, but those that are available suggest that trapping efficacy varies widely. Lewis and Macaulay (1976) compared the catch of six types of pheromone trap baited identically for the pea moth, *Cydia nigricana*. The magnitude of catch varied by a factor of 10, and direct behavioral observations of males showed that the efficiency of capture of males arriving within 2 cm of the trap varied from 12 to 48%. Some of these differences seemed to be explained by differences in the retentive properties of sticky traps and by the area of the trapping surface. Another important factor (considered explicitly in a following section) was the characteristics of the pheromone plume emanating from the trap.

Phillips and Wyatt (1992) advocated direct behavioral observations for determining how permutations of trap design alter trap catch. By simply varying the angle of entrance ramps to two types of sticky trap baited with food odor, catch of cockroaches was altered by a factor of about two. But the way in which catch was altered varied with ramp angle: few insects entered a trap with 60° angle ramp, but none escaped. All insects entered the 0° angle ramp, but half escaped. Such observations can guide improvements in trap design.

Elkinton and Childs (1983) compared the efficiency (the proportion of those males approaching the trap, what proportion that is captured?) for the gypsy moth of two trap types. Both types were baited with pheromone, (+)-disparlure. The "milk-carton trap," a trap with eight moth-sized entry ports, two on each side of the trap, was compared with the sticky wing trap. The milk carton trap is widely used in areas where gypsy moths are established because it has a collection capacity of hundreds of males, and its efficiency is not altered by the presence of males in the trap, except in the usual circumstance that there are so many males in the trap that their decomposition produces repellent odors (Elkinton, 1987). In contrast, the sticky surface of a wing trap is much less able to retain males once its retentive surfaces become paved with males and wing scales. Its efficiency therefore declines precipitously as males are captured.

The wing trap is similar in trapping principle to the sticky Delta trap now used for detection of gypsy moths in non-infested areas or for delimitation surveys of newly found, very low density invasions. In practice, the comparatively simple Delta trap should be ideal for survey and delimitation (provided its information is interpreted correctly) because, from a management perspective, presence of males versus their absence is the most salient information, provided that this information can be interpreted correctly. The capture of a single male signifies the need for a follow-up delimitation survey. The presence of several males is sufficient information for the manager to assume the presence of a nearby breeding population.

Elkinton and Childs (1983) found that milk-carton traps captured 10% of gypsy moth males approaching within 2 m of the trap and 44% of males contacting the trap; for fresh wing traps the proportions were 20 and 76%, respectively. Males that were not captured were observed to leave the test area, although one cannot be certain that they did not subsequently reorient to the trap. Assuming that the Delta traps and wing traps have similar trapping efficiencies, the relevance of such observations is quite apparent: if the trap could be modified to be more efficient, the sensitivity of the survey system should be enhanced, although by what factor cannot be inferred. Males that are not captured and depart from the vicinity of the trap may be subject to mortality or they may disperse beyond the effective range of the trap.

Evidence from mark-release-recapture trials with the gypsy moth (Elkinton & Cardé, 1980) suggests that the daily mortality plus emigration from the trap grid of males in a Michigan forest was 96%. When gypsy moth males fly in the absence of pheromone (ranging flight in "search" of a female), their trajectories appear to be random with respect to the direction of the wind (Elkinton & Cardé, 1983). Therefore, males that have not been captured on a given encounter with a trap may never be captured because of mortality or dispersal.

Effect of rate of semiochemical emission on capture efficiency. The effect of the rate of semiochemical emission has so far been considered for its effect on the extent of the downwind projection of the active space. Orientation of insects close to the odor source and, therefore, their capture in traps also are affected by the rate of emission. Some moths such as the oriental fruit moth (*Grapholita molesta*) are particularly attuned to a narrow band of emission rates (Baker & Cardé, 1979), which are close to the natural rate of female emission (Baker et al., 1980). Higher rates of emission diminish or eliminate trap catch (Figure 2) because of an antagonist effect on close-range orientation behaviors (Baker & Cardé, 1979). For other species such as the gypsy moth, trap catch and rate of pheromone are positively correlated (Figure 2), although trap catch may plateau at high emission rates (Cardé et al., 1977; Plimmer et al., 1977). Even in such cases where trap catch increases with rate of emission, it is not certain that higher rates of emission do not negatively ~~e~~ffect orientation at close range, causing a proportion of males to veer away from the trap before capture. Consequently, it would be possible to use a high emission rate to lure more insects to the trap's vicinity while simultaneously lowering the probability of capture by the trap.

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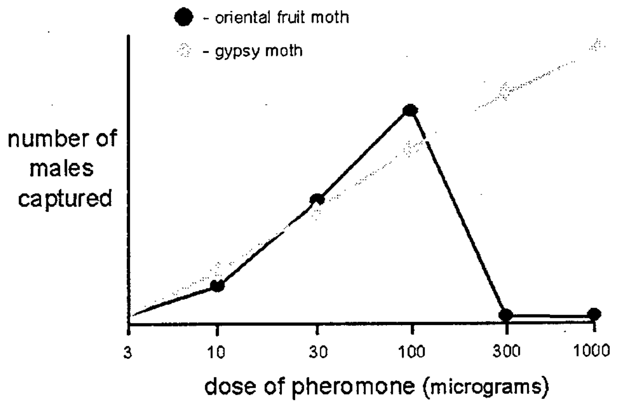

Figure 2. Effect of dose of pheromone in the dispenser on trap capture. For the oriental fruit moth (Grapholita molesta), capture peaks near 100 µg and declines sharply at higher doses (Baker & Cardé, 1979). For the gypsy moth (Lymantria dispar), trap capture increases gradually and reaches a plateau at the highest doses (Cardé et al., 1977; Plimmer et al., 1977).

Effect of fine-scale plume structure on capture efficiency. Orientation of male moths along pheromone plumes is governed, in part, by the fine-scale distribution of pheromone. Although definitive evidence is so far limited to several species, in those moths studied, encountering filaments at rates near 10 Hz causes a flight aimed more directly upwind accompanied by an increase in velocity (Mafra-Neto & Cardé, 1994; Vickers & Baker, 1994). Filaments of pheromone encountered at rates near 5 Hz or less tend to produce zigzag courses with little upwind displacement. Filaments with rates much below 5 Hz evoke casting or fail to promote sustained orientation.

The spatial features of the plume emanating from a trap also should affect trap capture, as first demonstrated by Lewis and Macaulay (1976) with the pea moth, *Cydia nigricana*. They documented characteristics of the plumes from six trap types with visible "smoke" tracers. The differences in the numbers of males lured to traps and those eventually captured were attributed in part to the boundaries, length and internal turbulent structure of the plumes. The same explanation likely applies to the differences among trap types in efficiency of catch of male gypsy moths, as documented by Elkinton and Childs (1983).

These case studies illustrate that altering trap design could produce substantial improvements in trapping efficiency. Such improvements might be accomplished by empirical field tests of design versus magnitude of catch, or, more usefully, by direct measurements of efficiency of capture in the field (Lewis & Macaulay, 1976; Elkinton & Childs, 1983) or in the wind tunnel (Foster & Muggleston, 1993). Another approach would be to characterize the fine-scale features of plumes released from traps by using a surrogate odor that can be readily measured. Propylene is a useful surrogate odor, and its density can be measured at high sampling rates with a photoionization detector (Justus & Cardé, 2002). So far we have less information on the close-range efficiency of traps used for true fruit flies, despite the extensive efforts underway to survey for their entry into the United States. Even a modest improvement in trapping efficiency might enhance their usefulness in detection.

Interpretation of Trap Catch

Empirical methods. There is extensive literature on the use of mark-release-recapture to establish the presumptive "attractive range" of semiochemical-baited traps. What such experiments generally have measured is the probability of capture of cohorts of insects released at various distances away from a single trap. In some procedures, insects are released in the presumptive downwind direction and in other protocols in a circular pattern surrounding the trap. It is generally not feasible to release insects while they are enveloped by a plume of semiochemical (but see the methods of Linn et al., 1986; Elkinton et al., 1987; Brady et al., 1989). Thus, in such range-of-attraction experiments, the distance over which an insect travels to a trap is a compounding of a) its survival and dispersal before entering the plume of semiochemical with b) its ability to find and enter the trap. The dispersal behavior and survival of an insect prior to its capture may well contribute more to the apparent range of the trap than the insect's ability to detect and follow a plume into the trap. From the perspective of interpretation of survey data, however, what remains relevant is the probability of capture at varying distances of initial dispersion from the trap.

A second general method for studying the range of influence of a trap involves the releases of insects into a grid of traps (Elkinton & Cardé, 1980). If the experimental grid has a very close placement of traps (on the order of 100 m spacing), then insects are released at points located in the middle of each square of four traps. This pattern produces release sites that are situated at a distance from the four surrounding traps that is 70% of the intertrap distance. If the intertrap distance is comparable to the spacing used in most surveys (on the order of 800 m or more), then insects are released evenly at as many sites in the area between the traps as operationally practicable. This method has the advantage of mimicking the recapture conditions encountered by insects that are evenly dispersed in survey grids. With this methodology, capture of male gypsy moths in 800 by 800 m (½ by ½ mile) grids was calibrated to show that 4% of the released males were captured. Information from an 80 by 80 m grid was used to verify that one major factor explaining the low proportion recaptured was the low day-to-day survival of males.

Simulation modeling. As valuable as mark-release-recapture methods are for developing an understanding of the meaning of positive and negative trap catch, such methods are very difficult to use in exploration of how differences in trap design, rate of semiochemical release, and trap placement alter probability of detection in surveys. Simulation modeling permits the systematic manipulation of various factors contributing to trap catch: the wind conditions dictating plume dispersal, general features of weather such as temperature, the rate of semiochemical release, trap density, and assumptions about insect dispersal and orientation behavior. For modeling to provide a reasonable simulation of the dispersion of plumes and insect behavior, it requires that we reproduce the physical features of the odorant plume in appropriate habitats and understand the particular insect dispersal and orientation strategies of the target species.

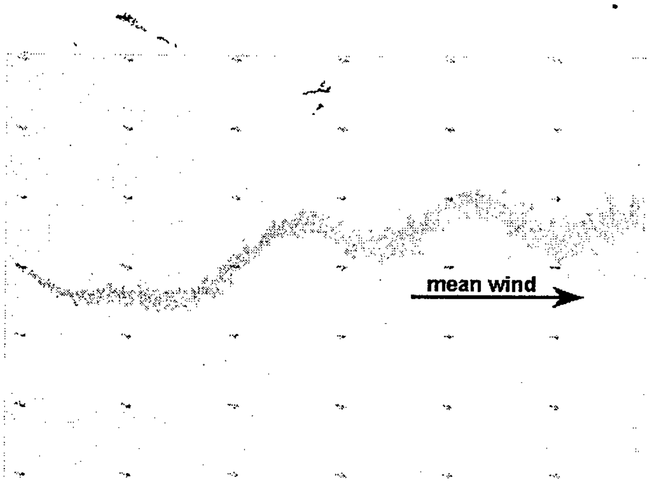

Figure 3. A simulation model of plume dispersion with a moderate level of meander (i.e. wind direction and velocity are relatively unvarying). Arrows depict instantaneous wind directions The dark areas indicate an above-threshold concentration of pheromone. The rate of pheromone emission and the threshold of response were set to match those of the gypsy moth (Lymantria dispar). The area represents a 60 by 100 m field (see Li et al., 2002).

Of course, models assume some compromises in simulation of the complexities of plume dispersion, and in behavior of insects in finding and navigating along a plume. To be computationally feasible, for example, the Li et al. (2002) model of plume dispersion and insect odor-location strategies operates in a planar world set at the height of the odorant source (Figure 3). The model neglects computation of the plume's vertical diffusion and possible vertical movement of the responding insect. This simplification is not entirely unreasonable in that many kinds of insects fly at relatively set heights above the ground, typically at heights that make contact with a plume from a natural source likely. Plumes do, however, disperse to some extent vertically, especially under some unstable (adiabatic) atmospheric conditions typical of midday (Fares et al., 1980), but also at night (Schal, 1982). Nonetheless, simulation modeling allows estimates of how improvements in trap range or efficiency of a trap might enhance detection protocols.

Future Directions

Semiochemical-based traps are widely used as sentinels for the arrival of many kinds of exotic invaders. Once such an invasion is detected, then such traps typically serve as the basis of a subsequent delimitation survey in which a grid of closely spaced traps is used to define the probable boundaries of an incipient population. Such demographic information can be helpful to the selection of a particular eradication strategy. Methods for design of survey traps generally have been to modify the trap's configuration by-trial-and-error and to vary the lure's emission rate, with the goal of producing the highest possible trap catch. The tacit assumption is that the trap design and lure giving the highest catch is an optimum combination for detection. The trap's efficiency of capture, which might be quite low, remains unknown with such approaches.

Research determining how the spatial pattern of trap catch in surveys relates to natural patterns of distribution and density relies largely on mark-release-recapture experiments. The validity of such protocols rests largely on the assumption that the released and introduced insects have comparable dispersal behaviors and abilities to find a lure-baited trap. In the case of Mediterranean fruit flies, some laboratory-reared flies do not appear comparable in semiochemical response to wild flies (Cayol, 1999), although, of late, the "competitiveness" of these flies has been improved. Despite these limitations, mark-release-recapture experiments nonetheless provide crucial information on how trap catch relates to natural densities.

A simulation modeling approach can generate information that would be difficult if not impossible to obtain through either behavioral observations or mark-release-recapture. Models allow for the systematic manipulation of changes in environmental conditions, trap range, capture efficiency, trap density and insect distribution, to see how changes in these parameters could alter the outcome of a survey. Estimates of the probability of detecting or missing various low-level populations can be based on many simulation runs of a given set of conditions rather than on the outcome of a single or several expensive field experiments.

Conclusions

Improvements in the technology of trapping are attainable with simple behavioral assays. Such improvements should lower the cost of surveys and enhance their reliability. Correlation of negative trap catch with the probability of missing an incipient infestation remains at the heart of survey interpretation. Mark-recapture protocols and simulation modeling are two techniques that should prove useful for improving patterns of trap deployment and interpretation of survey results.

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