

EXPLOITING THE INTERACTIONS OF CHEMICAL AND
VISUAL CUES IN BEHAVIORAL CONTROL MEASURES FOR
PEST TEPHRITID FRUIT FLIES

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ABSTRACT

Traps for tropical pest tephritids have relied primarily on chemical cues while traps for temperate pest tephritids have relied primarily on visual cues. Here we review research on the interactions between chemical and visual cues that have been observed in the development of traps for the tropical Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and the temperate apple maggot, *Rhagoletis pomonella* (Walsh). By exploiting these interactions, it may be possible to produce efficacious trapping systems that could be used in a behavioral approach to fruit fly population control.

Key Words: Tephritidae, *Ceratitis capitata*, *Rhagoletis pomonella*, trapping, pheromone, bait

RESUMEN

Trampas para plagas de tefrítidos tropicales han dependido principalmente de señales químicas mientras que trampas para plagas de tefrítidos templados han dependido principalmente de señales visuales. Se revisan investigaciones sobre las interacciones entre señales químicas y visuales que se han observado en el desarrollo de trampas para la mosca del Mediterráneo, *Ceratitis capitata* (Wiedemann), de lugares tropicales y para la mosca de la manzana, *Rhagoletis pomonella* (Walsh), de lugares templados. Aprovechando estas interacciones desde un enfoque de comportamiento, es posible crear sistemas de trampeo eficaces para controlar poblaciones de moscas de la fruta.

Trapping systems for insects are important components in integrated pest management programs. Trapping data are used to make decisions on the initiation or termination of control measures, as well as to assess efficacy of control approaches that have been implemented. With the availability of sufficiently effective traps that capture both female and male pest insects, trapping systems may be used as behavioral control measures and, thus, could be added to the growing list of biologically-based technologies for insect control (U.S. Congress 1995). Adults of tephritid fruit flies use visual and olfactory stimuli to locate hosts (reviewed in Prokopy 1986), and both visual and chemical cues have been used in traps for pest tephritid fruit flies (reviewed in Cunningham 1989a, Economopoulos 1989). Traps for tropical tephritids, such as the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), have relied primarily on chemical lures (Gilbert et al. 1984), while the traps for temperate tephritids, such as the apple maggot, *Rhagoletis pomonella* (Walsh), have used visual cues (Prokopy 1968). In this paper, we will 1) review fruit fly traps that use either chemical or visual cues alone, 2) discuss the interactions that may occur among different cues associated

with traps for fruit flies, and 3) explore the ability to exploit the interactions between these cues to provide powerful trapping systems for pest fruit flies.

CHEMICAL CUES AND VISUAL CUES USED INDEPENDENTLY

Chemical Cues

Some of the earliest trapping systems for pest fruit flies relied on the use of baits made from proteins and fermenting sugar (Gurney 1925). Numerous substances have been tested, and a corn protein hydrolysate was found to be most effective for capture of *C. capitata* (reviewed in Roessler 1989) while yeast hydrolysates were found to be most effective for *Anastrepha* species (reviewed in Heath et al. 1993). These baits are usually deployed in McPhail traps (Newell 1936), which are bell-shaped invaginated glass traps with a water reservoir, or other bucket-type traps (reviewed in Cunningham 1989a). These protein-baited traps capture both female and male fruit flies. Male-specific synthetic chemical attractants have been discovered for tropical tephritids in the genera *Ceratitis* and *Bactrocera* (reviewed in Cunningham 1989b). These attractants are called parapheromones because they cause responses similar to true pheromones, but they are not produced by the responding species. Trimedlure, *tert*-butyl 4 (and 5)-chloro-2-methylcyclo-hexane-1-carboxylate (Beroza et al. 1961), is a highly effective, commercially available parapheromone for male *C. capitata*. Methyl eugenol (Howlett, 1915) and cue-lure (Alexander et al. 1962) are parapheromones that are attractive to males of oriental fruit fly, *Bactrocera dorsalis* (Hendel), and the melon fly, *Bactrocera cucurbitae* (Coquillett), respectively, as well as other *Bactrocera* species. Parapheromone lures are typically mounted in Jackson traps (Harris et al. 1971), which are white triangular cardboard traps that contain a sticky insert placed on the floor of the trap (Gilbert et al. 1984).

Visual Cues

Fruit flies use a number of visual cues to locate hosts, and appropriate visual cues may be highly attractive to pest Tephritidae (e.g. Prokopy 1968). Numerous studies have examined the effect of shape, size and color of visual stimuli on fruit fly response (reviewed in Katsoyannos 1989). Prokopy (1968, 1972, 1973) demonstrated that more *R. pomonella* were captured on fluorescent yellow rectangles and on enamel red spheres than on other shapes in different colors. He hypothesized that the flat surface of the rectangle together with the fluorescent color represented leaf-type stimulus that elicits food-seeking and/or plant-seeking behavior, whereas spheres constitute a fruit-type stimulus that elicits oviposition and/or mating-behavior. More *C. capitata* were captured on yellow rectangles than light orange, light green, red, gray or clear rectangles (Prokopy and Economopoulos 1976). Nakagawa et al. (1978) tested response of *C. capitata* to a wide variety of shapes and colors. In tests among 7.5-cm spheres of different colors, black and yellow captured the most females and black, yellow, red and orange captured the most males. Among spheres, cylinders, rectangles and cubes of equal surface area (175 cm²) painted black or yellow, the black or yellow spheres caught the most of either sex. Among black or yellow spheres ranging in size from 1.5- to 18-cm diam, the black 1.5- and 3.2-cm spheres were two times more effective than equal sized yellow spheres, the black and yellow 7.5-cm spheres were equally effective, and the yellow 18-cm spheres were more effective than black 18-cm spheres. The yellow 18-cm spheres were most effective over all. Greany et al. (1977) found that fluorescent orange rectangles were the most effective for capture of the

Caribbean fruit fly, *Anastrepha suspensa* (Loew), and that most of the flies captured were sexually mature females (Greany et al. 1978). Sivinski (1990) found that more male *A. suspensa* were captured on 20-cm diam. orange spheres than spheres that were smaller or differently colored, but that female flies were trapped equally on 20-cm diam. green spheres. Green, yellow and orange were the most attractive colors for the Mexican fruit fly, *Anastrepha ludens* (Loew) (Robacker et al. 1990), but females preferred large spheres over large rectangles and small rectangles over small spheres (Robacker 1992).

CHEMICAL CUES THAT INTERACT WITH VISUAL CUES

Addition of Visual Cues to Chemical Cue-Based Standard Traps

In the section above, we discussed examples in which the chemical cues and visual cues were used independently of other cues. Protein baits are often used in glass McPhail traps, so the only potential visual cue is the brown color of the bait. Similarly, trimedlure is widely deployed in white Jackson traps and can also be used successfully in clear traps such as a Steiner trap (Steiner 1957, Nakagawa et al. 1971). Studies have shown, however, that the addition of a visual cue to these chemical cues can increase fruit fly capture. Liquid protein-baited glass McPhail traps painted fluorescent yellow captured more fruit flies than unpainted McPhail traps or McPhail traps painted enamel yellow, red or gray (Prokopy and Economopolous 1975). There are several plastic McPhail-type traps used currently in fruit fly detection that use a yellow base as a visual cue (e.g., Katsoyannos 1994). Similarly, use of a fluorescent color insert instead of a white insert in trimedlure-baited Jackson traps increased *C. capitata* capture during certain times of the year in field trials conducted in Guatemala (Epsky et al. 1996). Trimedlure-baited yellow panels are used in a high-density trapping protocol when outbreaks of *C. capitata* are detected in the continental United States (Lance and Gates 1994), an example of combining a yellow visual cue with the chemical cue to optimize fruit fly capture.

Addition of Chemical Cues to Visual Cue-Based Standard Traps

There is a complex of visual cues and chemical cues emanating from a host tree that could provide improved capture of fruit flies, especially female fruit flies. Females travel to host trees to find both food and oviposition sites. Females require protein to ensure fecundity (Christenson and Foote 1960) and volatile chemicals released from protein baits provide food cues to foraging females. One of the chemicals released from protein bait is ammonia (Bateman and Morton 1981). Prokopy (1968) and Moore (1969) found that addition of ammonia to red spheres did not increase capture of *R. pomonella* over unbaited red spheres, however ammonia did increase capture on yellow rectangles. Prokopy (1972) hypothesized that the addition of ammonia to yellow rectangles increased fly capture because the yellow rectangle elicits food-seeking response and did not improve capture on red spheres because red sphere elicits primarily oviposition and mating-related behavior.

Host fruit odor is a potential source of chemical attractants for females looking for an oviposition site. *Rhagoletis pomonella* adults are attracted to the odor of fresh-picked apples in the field (Prokopy et al. 1973), and to synthetic apple volatiles in laboratory bioassays (Fein et al. 1982). In tests conducted in apple orchards, addition of synthetic apple volatiles increased capture of flies when the lure was added to red spheres, but not when added to yellow rectangles (Reissig et al. 1982). These exam-

ples demonstrate the importance of using the correct chemical cue and visual cue combination for optimal fruit fly trapping.

Use of Chemical and Visual Cue Interactions to Develop New Trapping Systems

Pheromone Volatiles—Many of the tropical tephritids have male-produced pheromones that could potentially be powerful, specific attractants for female flies. Although a number of putative pheromone components have been identified and have shown activity in laboratory bioassays, they have generally been less than satisfactory in field tests (Howse and Knapp 1996). An exception to this has been found with the papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker, which does not respond to food-type lures such as protein (Landolt 1984) or sugar (Sharp and Landolt 1984). Males produce a pheromone that is attractive to females (Landolt et al. 1985) and chemical analysis determined that it is composed of a single component (Chuman et al. 1987). Although female flies responded to synthetic pheromone in flight tunnel bioassays (Landolt and Heath 1988), attempts to capture papaya fruit flies with synthetic pheromone alone were unsuccessful. Field observations noted possible attraction to the chemical, but that flies would land on papaya fruit near the lure. However, by combining the pheromone lure with an appropriate visual cue, i.e. a green 12.7-cm diam. sphere that mimicked a papaya fruit, a trapping system for these flies was developed (Landolt et al. 1988). Subsequent research found that a pheromone-baited green cylindrical trap could be as effective as a pheromone-baited sphere (Heath et al. 1996a).

Over 60 components produced by calling male *C. capitata* have elicited electroantennogram responses in female *C. capitata* (Jang et al. 1989). Black spheres baited with three of the major components (ethyl-(*E*)-3-octenoate, geranyl acetate and *E*, *E*- α -farnesene) captured more females than unbaited spheres in field tests conducted in Guatemala (Heath et al. 1991). In subsequent flight tunnel bioassays, addition of a fourth component (Δ -1 pyrolline) increased response of female flies over the three component blend, however, response was less than response obtained with calling males (Heath and Epsky 1993). Field tests of black spheres and cylindrical traps baited with these synthetic blends captured few flies relative to traps baited with the protein bait (R. R. H. and N. D. E., unpublished). Thus, there may be additional chemical cues, visual cues or other cues needed to develop pheromone-based traps for female *C. capitata*. Presence of competing male fruit flies and host fruit may be complicating factors (Howse and Knapp 1996).

Food Volatiles—We have been involved in developing food-based synthetic attractants for tropical pest fruit flies. Initial research involved a two component synthetic attractant containing ammonium acetate and putrescine, and a cylindrical trap to protect the lures from the environment (Heath et al. 1995). In field tests conducted in Guatemala with wild populations of *C. capitata*, interactions between chemical cues and visual cues were an important aspect of trap and lure development. In tests of clear traps versus traps with a painted color strip (~7.5-cm high) around the periphery of the middle to provide a visual cue, more female *C. capitata* were captured in green traps than clear traps, with intermediate capture in orange or yellow traps. More male *C. capitata*, however, were captured in yellow traps than orange traps, with intermediate capture in clear or green traps. We then compared green and orange traps baited with a low, medium or high dose of synthetic attractant, and liquid protein-baited McPhail traps. In these tests, capture of females in both orange and green traps baited with synthetic attractant increased in relation to McPhail traps as dose of the synthetic attractant increased. Females captured in these studies were dissected to determine mating status. Throughout these tests, 21-25% of the females captured in the

McPhail traps were unmated. However, 55 and 69%, respectively, of the females captured in the orange and green traps baited with the low dose of synthetic attractant were unmated. In the same traps baited with the high dose of synthetic attractant, percent unmated dropped to 13 and 4%, respectively. Thus, both the sex and the reproductive state of the fly affected response to the visual and chemical cue combination.

Quantification of Chemical and Visual Cue Interactions

Studies conducted by Aluja and Prokopy (1993) quantified the interaction between visual cue (color of fruit model) and chemical cue (concentration of synthetic host fruit odor) in host finding by *R. pomonella*. They found that a direct relationship between fruit odor concentration and fruit fly ability to find baited clear spheres (weak visual cue), but that fruit odor concentration had no effect on fruit fly ability to find baited red spheres (strong visual cue). Thus a high degree of interaction among cues may indicate that the cues being evaluated could be improved further. For example, in our research to optimize cylindrical traps baited with a two component food-based synthetic attractant (ammonium acetate and putrescine), we found numerous interactions between visual cues and chemical cues (Epsky et al. 1995) and we used this information to optimize the trapping system (Heath et al. 1996b). Cylindrical traps with the painted surface on the interior of the trap (presenting a smooth, shiny exterior to the fly) were compared with traps with the painted surface on the exterior of the trap (presenting a rough, dull exterior to the fly). Orange and green traps were baited with the medium and high dose of the two component synthetic attractant, as were tested in previous research by Heath et al. (1995). Significantly more females were captured on dull green traps than on shiny orange traps at either dose and slightly more females were captured on dull traps versus shiny traps of the same color. Additional interactions were observed in tests with change in putrescine dose. In initial studies, putrescine was formulated using polypropylene vials (1-cm i.d., 2.2-cm long). The vial formulation was then compared to membrane-based putrescine lures with an exposed membrane opening of either 3- or 5-mm diam. The exposed membrane opening governs the chemical release rate, so the lure with the 5-mm opening releases a greater amount of putrescine than the lure with the 3-mm opening. The putrescine formulations were tested in green cylindrical traps with either a shiny exterior or a dull exterior that were baited with ammonium acetate lures. Traps baited with ammonium acetate and membrane-based putrescine lures captured the most *C. capitata* males and females. Visual cue and chemical cue interactions were observed in that the best capture among the traps with the shiny green exterior was with the 5-mm putrescine lure and ammonium acetate lure, but among the traps with the dull green exterior the best capture was with the 3-mm putrescine lure and ammonium acetate lure.

Subsequent research discovered that trimethylamine is a potent synergist to ammonium acetate and putrescine for capture of *C. capitata* (Heath et al. 1997). Traps baited with all three components captured more flies than traps baited with ammonium acetate and putrescine, and this was true whether it was tested in clear (glass McPhail traps), light green, dark green or yellow traps (Heath et al. 1997, Epsky et al. 1998). Thus, increase in potency of the chemical attractant by the addition of trimethylamine lessened the interaction with the visual cue used in the trapping system. Presence of a visual cue is still an important element in optimal trap performance for traps baited with the three component attractant, however, choice of visual cue is less critical.

EXPLOITING INTERACTIONS FOR BEHAVIORAL CONTROL

Trapping systems have been developed primarily for use in detecting and monitoring target insects. There is an increasing need to move from insecticide-based control

measures to biologically-based control measures (U.S. Congress 1995), and the development of highly effective and selective trapping systems that target female fruit flies could provide a mechanism for behavioral control through mass trapping to be used alone and in conjunction with other integrated pest management systems. Experiments conducted in Greece indicated that populations of *C. capitata* could be effectively reduced when traps baited with liquid protein baits were deployed along with traps baited with trimedlure (Zervas 1996). Citrus fruit was protected from infestation by immigrating populations of *C. capitata* using mass trapping in combination with single-sex sterile male release (Economopoulos et al. 1996). In both studies, fruit was protected without insecticide application. Prokopy and Mason (1996) demonstrated protection of fruit from *R. pomonella* infestation by hanging sticky-coated red spheres in close proximity to synthetic fruit odor and synthetic food odor around the periphery of an apple orchard to intercept fruit flies immigrating into the orchard.

Although showing promise, these trapping systems do not provide the longevity necessary for use in long-term, mass trapping applications. Either sticky material or a water reservoir is used to kill attracted flies. Sticky surfaces quickly become deactivated by the accumulation of target and non-target insects on the surface, as well as by dust and debris that might be blown onto the trapping surface. Water-filled traps may dry out or become filled with captured insects. The ideal mass trapping system would last for 6-8 weeks and be essentially maintenance free during that time period. An alternative approach is the incorporation of a pesticide instead of the sticky material with the dry trap. A dry trap with the parapheromone methyl eugenol, mixed with a pesticide, was used successfully to eradicate the oriental fruit fly in a male-annihilation project (Steiner et al. 1965). Methyl eugenol is a feeding stimulant as well as an attractant. Thus, oriental fruit fly males consume the pesticide-laden formulation and obtain a lethal dose of pesticide. We developed a toxicant system that included a combination of visual cue, feeding stimulant and a pesticide in a formulation that could be applied in a relatively easy manner for use in traps as an alternative to sticky material (Heath et al. 1995). Panels coated with this material were placed inside a cylindrical trap to kill flies that have entered the trap. This toxicant system is deactivated if it is exposed to rain, thus compromising its use on the exterior surface of a trap (Duan and Prokopy 1995a, 1995b). Recent research has been directed towards the development of weather resistant, spatially localized toxicant-based bait stations. The incorporation of a pesticide with female-targeted synthetic attractants and well designed traps with appropriate visual cues into pesticide-bait stations would provide powerful tools not only for monitoring but potentially for fruit fly suppression that would avoid the environmental problems of pesticide bait sprays.

The availability of food-based synthetic attractants will afford a new dimension in exploring the interactions among visual cues and chemical cues for pest fruit fly females. Previous efforts with food-based liquid protein baits were hampered by batch to batch variability as well as by change in attractiveness of the bait over time (Epsky et al. 1993, Heath et al. 1994). Liquid baits require use of a trap with a reservoir, thus the ability to investigate interactions among chemical cues and visual cues using these lures is limited. Increased knowledge of behaviors associated with attraction of both sexually immature females and egg laying females will improve detection and delimitation of pest fruit flies, and provide increased protection of crops adversely affected by their presence.

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