

PHEROMONES AND PARAPHEROMONES IN THE
CONTROL OF TEPHRITIDS

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ABSTRACT

The complex lives of tephritids are mediated by a variety of chemical cues. Those involved with feeding, host location, mating, and oviposition have been used in control. *Feeding*—recent work suggests that tropical adult fruit flies feed for the most part on leaf surface bacteria. New attractants based on bacteria and their by-products may soon be available. *Host location*—host odors, colors and shapes can attract flies and are presently used in integrated pest management. These stimuli are frequently added to traps baited with sexual pheromone and parapheromones. *Mating*—males, particularly in lekking species, release pheromones that attract both males and virgin females. These compounds are produced in a morphologically broad range of glands. Parapheromones are compounds, often originally derived from plants, that attract sexually mature males and more rarely, females. Their role in fruit fly bionomics is unknown, though they may coincidentally resemble pheromones or be pheromone precursors. The principal uses of sex attractants have been in male eradication and monitoring; however, in the future they may also be useful in quality control. *Oviposition*—females in a number of pestiferous species mark oviposition sites with a pheromone that discourages egg laying by subsequent females. Chemical identification of these substances has proved difficult, but field trials suggest that they may be used to protect fruit crops.

RESUMEN

La vida compleja de tephritidos es regulada por una variedad de apuntes químicos. Aquellos envueltos con la alimentación, localizar hospederos, apareamiento, y oviposición se han usado para su control. *Alimentación*—reciente trabajo sugiere que moscas adultas tropicales se alimentan en su mayor parte de bacterias en la superficie de la hoja. Nuevos atrayentes basados en bacterias y sus productos secundarios, pudieran estar disponibles muy pronto. *Localizar hospedero*—olor del hospedero, colores y formas pueden atraer moscas y son actualmente usadas en la administración integral de plagas. Estos estímulos son frecuentemente añadidos a trampas cebadas con feromonas sexuales y con paraferomonas. *Apareamiento*—machos, particularmente en las especies "lekking" echan feromonas que atraen a machos y hembras vírgenes. Estos compuestos son producidos por un número de glandulas morfológicamente diversas. Las paraferomonas son compuestos que a menudo originalmente se derivaron de plantas, y que atraen a machos sexualmente maduros y más raramente a las hembras. Su función en la bionomía de las moscas de frutas es desconocida, aunque ellas pueden coincidentalmente parecerse a las feromonas o ser precursoras de feromonas. El uso principal de los atrayentes sexuales ha sido en la erradicación y chequeo de los machos, sin embargo, en el futuro ellos también pudieran ser útiles en el control de calidad. *Puesta de huevos*—las hembras, en un número de especies de plagas, marcan el lugar donde ponen los huevos que desalenta a otras hembras de poner huevos. La identificación química de estas substancias ha probado ser difícil pero pruebas en el campo sugieren que ellas pudieran ser usadas para proteger los cultivos de frutas.

On an arthropodean scale, the lives of fruit flies can be extraordinarily eventful. Some superlatives include: learning of host plants and pheromones (Prokopy et al.

1982a, Roitberg and Prokopy 1981), regular dispersions to feeding areas up to 100 km away (Drew et al. 1984), intricate dual-strategy male mating systems with elaborate lek centered courtships and highly discriminating females (Burk 1981, Sivinski and Burk 1986) and the exploitation of chemically and morphologically complex bodies (fruit) for larval development.

Much of this behavioral exuberance is mediated through chemical cues and this in turn offers a number of opportunities for control through chemical manipulation. Entomologists concerned with the attraction/repulsion of tephritids have concentrated their efforts on fruit fly feeding, host location, mating and oviposition. Only the latter two involve pheromones (*sensu strictu*). However, much of tephritid control has been and remains to be done with feeding/host cues. Since these kairomones are often applied in parallel to and conjunction with pheromones and parapheromones, they deserve some brief discussion here as well.

ADULT FEEDING

Tephritids feed on extrafloral nectaries, sap flows, bird dung and occasionally flowers (i.e., *Dacus curcurbitae* Coq.; Bateman 1972). However, most were thought to subsist on homopteran honeydew (e.g., Hagen 1958). Australian work on *Dacus* spp. has challenged this assumption and reemphasized the role of leaf surface bacteria in diet, particularly the diet of species in the humid tropics where conditions do not allow the accumulation of insect excretions (Drew et al. 1983; Courtice and Drew 1984; see also work on *Anastrepha fraterculus* (Wied.) by Malavasi et al. 1983). The large numbers of bacteria in tephritid crops have been noted for many years, but were thought to be largely symbionts (Petri 1910). Now these microbial masses are being reinterpreted as the result of consumption and a new generation of bacterial based attractants may be in the wings, although some controversy exists regarding the present work.

In the meantime, bacteria are being exploited in food traps. Commonly used protein hydrolysate baits apparently owe much of their attractiveness to the bacteria they nurture. Gow (1954) noted that the addition of antibiotics lowers the effectiveness of protein lures and Morton and Bateman (1981) found ammonium, probably the result of bacterial degradation, to function as the principal attractant in such solutions (see also, Courtice and Drew 1984). Amino acids act as feeding stimulants once contact is made (for similar effect in *Anastrepha*, see Sharp and Chambers 1983).

Food baits are used in both population monitoring and control. The standard liquid filled trap is the McPhail trap, an invaginated glass bottle based on an ancient Chinese design for the capture of blow flies. These have been particularly useful for detection of *Anastrepha* spp., for which no other practical attractant exists. Sprayed mixtures of protein bait and insecticide (typically malathion, which is relatively nontoxic to mammals, or naled) are classic means of tropical tephritid control (see Drew et al. 1978). In temperate regions, poisoned protein hydrolysates have not always proven more effective than insecticides alone in controlling *Rhagoletis* spp. (Reissig 1977).

HOST LOCATION

Plants and their fruits can be conspicuous by their shape, color, and odor. Location of hosts by their specific shape seems rare, although *Platyparea poecoloptera* (Schrank) are attracted to asparagus-like and *Urophora affinis* Fraunfeld to composit-like forms (Eckstein 1931, Zwolfer 1970). The apple maggot, *Rhagoletis pomonella* Walsh, is drawn to fruit-like spheres and circles (see Prokopy and Roitberg 1984 for recent discussion). *R. pomonella* is attracted to apple volatiles (Prokopy et al. 1973, Fein et al. 1982), and synthetic apple volatiles increase the performance of traps (Reissig et al. 1982,

Swift 1982). Host odors also lure the olive fly, *D. oleae* (Gmelin) (Fiestas Ros de Ursinos et al. 1972). Contact arrestants and repellents of *Rhagoletis* spp. occur in host and nonhost tissue, respectively (Bush et al., cited in Prokopy 1977). A number of plants produce chemicals attractive to tephritids, but often their role, if any, in fruit fly bionomics is obscure (Keiser et al. 1975; see discussion of parapheromones below).

This is an appropriate point to mention the role of color in control. Wavelengths reflected from foliage and fruit can be highly attractive. *Rhagoletis* spp. are drawn to fluorescent yellows, and sticky yellow boards alone suppress populations in cherry and blueberry (Prokopy 1976, Boller and Remund 1981). Sticky red spheres are also useful against apple maggot and have been used in integrated pest management procedures (Prokopy 1975, 1985). *Ceratitidis capitata* (Wied.) and *Dacus* spp. (with the exception of *D. cucurbitae*) are lured to yellow, while *Anastrepha suspensa* (Loew) is most attracted by orange, (Bateman 1976, Greany et al. 1977, de Souga et al. 1984). Striping in the case of *A. suspensa* and checkering in *D. tryoni* (Froggatt) increased the effectiveness of colored decoys (Davis et al. 1984, Hill and Hooper 1984).

Traps containing food, host, or sexual lures are often colored as well, although in the case of the olive fly, *D. oleae*, yellow did not boost the value of MacPhail traps until a sticky compound was placed on the outside (Bateman 1976, Prokopy and Economopoulos 1975). This emphasizes the importance, when designing traps, of understanding the behavior of flies as they approach and land upon a surface. Davis et al. (1984) found that Caribbean fruit flies generally landed on the underside of foliage and thus modified the Jackson trap (a folded cardboard tent with an inserted floor) so that there was a ceiling adhesive. Mediterranean fruit flies tend to land on upper surfaces and walk to lower surfaces. This suggests that an upper surface adhesive placed on floor inserts of a Jackson trap is the most efficient means of trapping this species (Hendrichs and Aluja, personal communication).

MATING—PHEROMONES AND PARAPHEROMONES

The meeting of the sexes is not a simple procedure in the Tephritidae, particularly among polyphagous tropical and subtropical species. Host unpredictability has placed a selective emphasis on males' advertising their qualities to passing females rather than searching fruit for available mates (Burk 1981, Prokopy 1980, Sivinski and Burk 1986). Males of these tropical species frequently aggregate in leks where intense competition has further elaborated their distance signals and courtship displays. In *Anastrepha*, *Ceratitidis* and *Dacus* there are acoustic, visual, and pheromonal signals directed at mate-searching females (e.g. Sivinski et al. 1984). This barrage of male-produced stimuli complicates the study and manipulation of any one signaling system.

Another complication in the application of pheromones for control arises from the lek mating system. Males who join mating aggregations are believed to have a greater probability of inseminating a female. They are therefore attracted to the signals of other males. A rule-proving exception is the nonlekking *Rhagoletis cerasi* L. where male pheromone is not attractive to other males; (see Katsoyannos 1982). On the other hand, while temperate females mate every week or less, tropical females tend to copulate much less frequently, perhaps only once in a lifetime (Bateman 1976, Prokopy and Roitberg 1984). Thus the proportion of the female population responding to sexual signals at any one time can be quite small (Burk and Calkins 1983), especially in comparison to food baited traps which tend to attract more females (1.4 to 1.8X in Caribbean fruit fly, Perdomo et al. 1976). Often, pheromones and parapheromones are referred to as "male lures". This is an overstatement. When equal numbers of males and *receptive* females are exposed to male baited traps they are captured in roughly equal numbers (Perdomo et al. 1976). This propensity for sexual attractants in the field to capture males

but not females influences control strategies, as we shall see later.

As implied earlier, attractant pheromones in tropical frugivorous tephritids are emitted by males; with the exception of *D. oleae*, where both sexes produce similar pheromones (Baker et al. 1980, Mazomenos and Pomonis 1982). Those that have been identified, at least in part, tend to be multicomponent blends (Baker et al. 1982, Gariboldi et al. 1983, Nation 1983, Battiste et al. 1983), and may include substances active at either close or long ranges (Bellas and Fletcher 1979). The bizarre papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker, appears to be exceptional in possibly having only a single component pheromone (Landolt et al. 1985). Many *Dacus* spp. puff out "smoke"; red or orange inorganic phosphate crystals coated with long chain hydrocarbons (C25-29) that resemble cuticular waxes (Ohinata et al. 1982). It is possible these evolved as a means of projecting nonvolatile cuticular contact pheromones and so expanded the flies' broadcast range. One might wonder if the color of smoke has a communicative function as well.

Different genera have evolved a variety of pheromone glands; in *Dacus*, male and female glands are located in the rectum. In *Anastrepha*, large glandular cells are present in the pleural region of the abdomen. There also are sexually dimorphic salivary glands. In *Rioxa pornia* (Walker), there are similar pleural and salivary glands from which in the latter case. A foam (with pheromone ?) is produced that females consume during copulation. In medfly, pleural glands and dimorphic salivary glands are combined with ductless glands in the last abdominal segment. Finally, in *Rhagoletis* there are no specialized glands but pheromones may arise in the gut (Nation 1981).

Pheromones are perceived in *D. tryoni*, the Queensland fruit fly, by sensors on the antennae, maxillary palps, and last segment of the ovipositor (Giannakakis and Fletcher 1981, Metcalf et al. 1983). If such a receptor topography is general it might account for a peculiar behavior noted in Caribbean and Mediterranean fruit flies. Females often sit on the undersides of leaves with their ovipositors stuck upward perpendicular to their bodies. The action seems purposeful but puzzling. Can sensillae on the ovipositor pick up airborne chemicals and could it be erected to act as a sort of third antenna?

The range of fruit fly pheromones show considerable variance. Those of *D. tryoni* and *D. neohumeralis* attract males from several meters away (Bellas and Fletcher 1979). The pheromone of *D. oleae* works well at 80 m (Delerio et al. 1982), while the medfly synthetic attractant, trimedlure, is effective to at least 20 m (Delrio and Zumreoglu 1982). The champion is another parapheromone, methyl eugenol, which attracts Oriental fruit flies, *D. dorsalis*, from distances of up to 1 km (Steiner 1969).

Parapheromones, such as the above mentioned methyl eugenol and trimedlure, are something of a mysterious blessing (Table 1). Often as not, they have been discovered by accident and are frequently, but not always, derived from plants (kerosene was a

TABLE 1. THE MAJOR PARAPHEROMONES USED IN FRUIT FLY CONTROL—FROM CHAMBERS (1979).

Compound	Pest species for which used
Methyl eugenol	Oriental fruit fly, <i>Dacus dorsalis</i> ; Mango fruit fly, <i>D. zonatus</i>
Cuelure 4-(p-hydroxyphenyl)- 2-butanone acetate	Melon fly, <i>D. curcubitae</i> ; Queensland fruit fly, <i>D. tryoni</i>
Trimedlure <i>tert</i> -butyl 4 (or 5)-chloro-2-methyl- cyclohexanecarboxylate	Mediterranean fruit fly, <i>Ceratitidis capitata</i> Natal fruit fly, <i>C. rosa</i>

favorite at the turn of the century, Severin and Severin 1915). Methyl eugenol was found to be the active ingredient in the classic attractant, citronella oil, while the essential oils of the seeds of *Angelica archangelica* L. were popular medfly attractants before the discovery of trimedlure (see citations in Guiotto et al. 1980). Ether extracts of any number of plants can attract flies (61 of 232 in Keiser et al. 1975). In the case of the Australian plant *Zieria smithii*, whose crushed leaves attract *D. cacuminatus* (Hering), its essential oils are ca. 85% 0-methyl eugenol (Fletcher et al. 1975). It is believed that the majority of such plants do not serve as food, shelter, or mating sites but since the natural histories of most tephritids are poorly known, it is probably premature to make such a generalization.

Parapheromones undoubtedly fill some sexual role. Females of some *Dacus* spp. respond to them at the same time and in much the same manner as they would to pheromone (Fitt 1981a). Mediterranean and Oriental fruit fly females will even be attracted to parapheromones in the field when their males are trapped out (Steiner et al. 1965, Nakagawa et al. 1970). To females they are apparently something like a pheromone, but do not compete well with the real thing. There is certainly little species specificity in parapheromones. Seventy-nine species of *Dacus* in the South Pacific are attracted by either cuelure or methyl eugenol (Drew 1974, Drew and Hooper 1981; only the jackfruit fruit fly *D. umbrosus* F. responds to both, Umeya and Hirao 1975).

The reaction of males to parapheromones both substantiates and obscures their status as pheromonal surrogates. Males are more attracted to parapheromones as they mature sexually but in at least some *Dacus* spp. they are most responsive at the time of day opposite their peak period of sexual activity (Brieze-Stegeman et al. 1978, Fitt 1981b). Once males arrive at a methyl eugenol site they "pulse" their mouthparts and lick the lure. Fitt (1981b) has found metabolites of methyl eugenol in the pheromone of *D. tryoni* 24 h after ingestion, which suggests it may be a pheromone precursor that is sought by males when available but which is not strictly necessary for pheromone production. A somewhat similar case may occur in neotropical euglossine bees, many of which are specialized pollinators of orchids. Males visit flowers solely to gather floral scents from which to construct pheromones and some are highly attracted to eugenol (Williams and Whitten 1983). Unfortunately the generality of the argument is shaken by the relative unpalatability of trimedlure. It is preferable to use fumigant insecticides in conjunction with trimedlure since the insects are not likely to eat it (Drew et al. 1978).

Whatever the role of parapheromones in tephritid biology it is believed that there is room for improvement in fruit fly attractants. Methyl eugenol is more effective at trapping the Oriental fruit fly than trimedlure is in capturing Mediterranean fruit fly. This suggests to Fletcher (1977) an untapped responsiveness in the medfly. Early work with *C. capitata* sex pheromone shows it to be at least as effective as trimedlure, and bears the promise of further improvement (Zümreoglin 1983). Fletcher (1977) also notes that the pheromone of *D. tryoni* is more successful than the classic parapheromone attractant, cuelure. All of this presages the arrival of more effective baits with further research. There is a particular sense of urgency concerning lures for Oriental fruit fly since methyl eugenol has recently been found to cause liver cancer in rats (Mitchell et al. 1985).

What can be done with available lures? As noted, tropical fruit fly attractants catch mostly males. Even so, male annihilation through lure/toxicant mixtures have eradicated Oriental fruit fly from a number of islands (Koyama et al. 1984; note these authors found that male numbers must be suppressed to 1% of their former level before there is a detectable fall in fruit infestation). Suppressions of wild males is, of course, useful before a sterile release. There is extensive literature on how, when and where to apply lure/toxicant mixtures. The interested reader should consider the following and their bibliographies: Nakamori and Soemori (1981), Chambers (1977, 1979), Drew et al.

(1978), Boving et al. (1980), Hart et al. (1966), Barclay and van den Driessche (1984), Cunningham et al. (1975). Also, note subsequent citations under discussion of monitoring since there is considerable overlap in techniques. Pheromones and parapheromones have proved to be particularly useful in monitoring populations and warning of introductions. For instance, methyl eugenol has discovered and aided in the eradication of at least 11 forays of Oriental fruit fly into Los Angeles County, California (Anonymous 1984). An introduction to the literature is as follows: trap design and presentation of the lure (Drew et al. 1978, Hooper and Drew 1978, Ibrakin et al. 1979, Jones et al. 1983, King and Landolt 1984, Nakagawa et al. 1979, 1981, Rice et al. 1984, Leonhardt et al. 1984, refer to earlier discussion of host cues for further trap literature) lure mixture (Hooper 1978), and height placement of traps (Holbrook and Fujimoto 1969, Hooper and Drew 1979). Pheromones may have an expanding role in quality control, i.e. making sure that domesticated sterile flies can respond to sexual signals in a competitive manner (Boller et al. 1981).

OVIPOSITION

A female fruit fly puts its eggs into a closed environment. Beneath the fruit surface can lurk hidden con- and heterospecific competitors (note that *D. dorsalis* larvae can suppress the development of *Ceratitidis capitata*; Keiser et al. 1974). Numerous larvae in a single small fruit would destroy the fruit before maturity; thus, multiparasitism would be detrimental. It behooves the first female to oviposit in a fruit to advertise the fact and subsequent females to heed the warning. This has led to the evolution of oviposition deterring pheromones in all of the major pestiferous fruit fly genera (Prokopy 1981).

As might be expected, the greater the potential for competition the more developed such marking systems become. For instance, in the western cherry fruit fly, *Rhagoletis indifferens* Curran, the natural host can support a single larva and the marker is quite effective in discouraging further egg laying (Mumtaz and Alinizee 1983). At the other extreme the melon hosts of *D. curcubitae* can support hundreds, even thousands, of larvae, and females do not use oviposition deterring pheromones (Prokopy and Koyama 1982). In *A. fracteculus* females put more marker on smaller fruit, thereby investing more material to avoid more acute competition (Prokopy et al. 1982b).

These pheromones have, for the most part, resisted chemical analysis, though in *D. oleae* the marker is simply olive juice from the oviposition puncture smeared over the fruit by the fly (Cirio 1971, Prokopy and Roitberg 1984). In this case, the actual repellent chemical resides in the oil fraction (Girolami et al. 1981). In *R. pomonella*, at least one major component is produced in the posterior of the midgut (Prokopy et al. 1982c). There can be cross specific recognition of oviposition deterring pheromones (Averill and Prokopy 1982).

Under laboratory conditions the pheromones of some species can persist for up to 12 days, but their effective duration in the field is much less (Katsoyannos 1975). However, older larvae are not "invisible" to foraging females. *D. tryoni* can recognize occupied fruit pulp by its chemical composition, even after larvae are removed (Fitt 1984). *A. suspensa* senses larval feeding sounds and prefers to lay eggs on silent sites (Sivinski, unpublished data).

Once identified and synthesized, oviposition repellents could be an attractive means of control (Prokopy 1972). To date, individual cherry trees have been effectively protected from *R. cerasi* by deterring pheromones (Katsoyannos and Boller 1980). However, a potential drawback is that these "warnings" tend to lose force as hosts become scarce and females are deprived of opportunity to oviposit (Mumtaz and Alinizee 1983, Roitberg and Prokopy 1983). In *R. pomonella*, females encountering marked fruit are

more likely to disperse relatively long distances (Roitberg et al. 1984). One can imagine circumstances in which increased dispersion from a localized infestation would be counterproductive to control. Note that deterring pheromones serve as a kairomone of the *Rhagoletis* egg parasite *Opius lectus* Gahan, and so might serve to concentrate natural enemies (Prokopy and Webster 1978).

We hope this brief review has introduced the reader to some of the problems and solutions in controlling fruit flies through pheromones and parapheromones.

END NOTE

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