

NECTAR-RELATED OLFACTORY AND VISUAL ATTRACTANTS FOR MOSQUITOES

WOODBRIDGE A. FOSTER AND ROBERT G. HANCOCK

Department of Entomology, The Ohio State University, Columbus, OH 43210

ABSTRACT. Mosquitoes commonly feed on plant nectar and other sugar sources, which they locate chiefly by visual and chemical cues. A summary of current evidence indicates that nectar sources are not as attractive as blood sources at specific times in a mosquito's life but that sugar feeding is usually necessary and more frequent than bloodfeeding. Plant attractants used in traps would have the advantage of being effective for both sexes, starting soon after emergence, and for blood-digesting, gravid, and gonoinactive females. Field studies suggest that mosquitoes are most attracted to light-colored flowers, but the independence of appearance from fragrance has not been firmly established. Volatile components of flowers and honey have been proven to be attractive, but in a preliminary field trial honey extract was less attractive than some blood-host kairomones. Terpenoids and aromatics provide many of the distinctive and dominant volatiles of flowers; they elicit both chemosensory and behavioral responses in mosquitoes.

INTRODUCTION

Both sexes of mosquitoes feed on plant sugars. The ubiquity of this activity has been verified by researchers directly observing mosquitoes feeding on sugar sources in the field, detecting plant sugars in the diverticula of field-caught mosquitoes, and examining sugar-feeding behavior in the laboratory. The sugar sources utilized include a wide variety of natural ones, including floral and extrafloral nectaries, homopteran honey dew, aging or damaged fruit, healthy and damaged plant parts, and regurgitates of ants. Artificial sources include sugarcane trash and the sugaring stations of moth collectors. These sources appear to be located by the mosquitoes not by chance but by orientation to visual and chemical cues associated with the presence of sugar. Therefore, it appears possible that these stimuli can be put to use, either in monitoring or controlling mosquito populations, provided that they attract large numbers to traps.

The practical effectiveness of sugar-related attractants is difficult to predict. There is conflicting evidence and opinion about which mosquito genera and species require sugar or feed frequently on it, and there remains the persistent notion that males need sugar more than females do. There are also questions about the age and physiological state when mosquitoes are most likely to take sugar and about the attractive power of sugar-host stimuli compared to those of blood hosts. Any of these aspects of attractants can be critical to their effectiveness for adequately monitoring or reducing local populations. We will address these points briefly (without comprehensive citations; see Yuval [1992] for recent review) before discussing the attractants themselves.

BENEFITS OF SUGAR FEEDING

The benefits of sugar feeding to mosquitoes have been demonstrated in the laboratory. Energy reserves at emergence allow survival for only a few days. Sugar meals provide the necessary energy for both survival and flight during the mating period and until the female can find vertebrate blood (Van Handel 1965, Nayar and Van Handel 1971, Nayar and Sauerman 1975a). The blood meal contributes energy for survival and flight, in addition to its role in allowing egg development in anautogenous mosquitoes. Reciprocally, a substantial energy reserve, the result of previous sugar feeding, enhances the size of the egg clutch (Nayar and Sauerman 1975c, Foster et al. 1989). Sugar that is supplemented with amino acids, as commonly occurs in nature (Baker and Baker 1983), extends adult life beyond that on sugar alone (Eischen and Foster 1983). Therefore, sugar appears to promote mosquito fitness in several ways.

Sugar feeding also can be detrimental, in that a mosquito's crop, if engorged with sugar from a recent meal, limits the volume of blood imbibed, thus reducing the egg clutch (Foster et al. 1989). Perhaps because of this effect, recent sugar feeding typically inhibits responses to blood hosts (Khan and Maibach 1970, Jones and Madhukar 1976), thus delaying the onset of the next gonotrophic cycle. Mosquitoes also incur lost time and risks while locating and feeding on natural sugar sources.

Determination of the extent to which mosquitoes actually sustain these benefits and losses in nature is problematic. It is difficult to assess and/or vary the availability of sugar under field conditions, then measure the mosquito's con-

sequent behavior and reproductive output. At present, the significance of sugar feeding in nature must be inferred from its prominence in mosquito nutrition there.

BIOLOGY OF NECTAR FEEDING

Species: Nearly all mosquito species investigated have been found to feed on sugar in nature. However, in a few species sugar feeding appears to be rare or absent (Muirhead-Thomson 1951, Edman et al. 1992). For other species sugar can be essential to the early stages of adult maturation or egg development (Volozina 1967, Andersson 1992), and some cannot survive on blood alone, no matter how frequently it is taken (Downes 1958; Nayar and Sauerman 1971; Foster, unpublished data). Autogenous species are often incapable of developing a clutch of eggs without sugar (O'Meara 1987). Probably most mosquitoes depend on sugar to supplement blood feeding, and the exceptions live where blood is always close and relatively risk-free, providing a reliable energy source.

Sex: The literature indicates tremendous variation in the sex ratio of mosquitoes at sugar sources or testing positive for sugars. Male or female bias may be a consequence of small or focal samples. It can also reflect different diel sugar-feeding times (McCrae et al. 1969) or progressive stages of aging of a brood, the males emerging first, staying closer to breeding sites, then dying first (Magnarelli 1977). Attempts are rarely made to determine simultaneously the sex ratio of the local base population. The bulk of the data indicates that the 2 sexes are nearly equal in their utilization of sugar or that males take it moderately more often, a consequence of their intense swarming activity.

Age: When the age structure of sugar-feeding mosquitoes is compared with the background population, it is evident that sugar feeding is similarly likely to occur at any age (Magnarelli 1978, Nasci and Edman 1984, Foster 1986, Reisen et al. 1986, Haramis and Foster 1990). Sugar feeding soon after emergence is common; it precedes dispersal, mating, and blood feeding (Haeger 1955, Service 1977, Nayar 1981, Magnarelli 1983), and can be a necessity for these activities. This would explain reports of higher proportions of nulliparous females among nectar feeders than blood feeders (Vargo and Foster 1984). But greater nectar feeding among parous females has also been recorded (Andersson 1990). It is safe to assume that most mosquitoes begin adulthood by sugar feeding and then continue it at some regular rate, regardless of chronological or reproductive age.

Gonotrophic state: Sugar feeding can occur during any phase of the gonotrophic cycle: empty, blooded, or gravid. Most direct studies of nectar feeding, which usually indicate a paucity of blooded females and preponderance of empty ones, have not compared the samples with the base population. Without population information, it is impossible to discriminate among sources of bias in the composition of the nectar-feeding sample. The assay of nectar content may be free of this bias, but it is an unreliable indicator of recent sugar feeding, because sugar digestion proceeds more slowly while the midgut contains blood (Miles 1977,¹ Foster 1986). Among direct observations of sugar feeding that included a comparison with the background population, some species nevertheless showed a strong bias against sugar feeding in the blooded state and a moderate bias against it in the gravid state (Foster 1986), but other species took sugar without regard to gonotrophic state (de Meillon et al. 1967, Reisen et al. 1986). Data based on sugar content are equivocal on these points (Volozina 1967, Nayar 1978, Nasci and Edman 1984, Foster 1986, El Akad et al. 1989, Andersson 1990, Jaenson and Ameneshewa 1991).

Laboratory observations of several genera indicate that there is wide variation in the extent to which blood digestion inhibits sugar feeding (Foster 1986), and energy-reserve status modulates the expression of sugar feeding during the gravid state (Hancock and Foster 1993a). We conclude that blooded and gravid females are sometimes underrepresented in sugar-feeding collections, but the extent will vary with species and energy status.

Reproductive diapause: Those species overwintering as adults are typically nonbloodfeeding and gonoinactive, but accumulate extensive fat reserves in late summer and autumn, often assumed to be the result of sugar feeding. Some field studies indicate that diapausing females nectar feed at the same rate as gonoactive ones (Reisen et al. 1986), or even at a lower rate (Jaenson and Ameneshewa 1991), but Bowen (1992a) demonstrated in the laboratory a significantly higher sugar-feeding activity of diapausing females. Differences probably are related to particular climatic conditions.

Feeding frequency: The actual frequency of sugar feeding has not been precisely determined, though commonly it may be higher than blood-feeding (O'Meara 1987). From fluctuations of

¹ Miles, C. T. 1977. The effect of blood, nutritional reserves and age on the rate of crop sugar depletion in the mosquito *Aedes aegypti* (L.). M.Sc. thesis. Ohio State University, Columbus.

sugar content in synchronized cohorts, some authors have inferred the presence of 3-day (Nayar 1981) or 7-19-day (Morris 1984) cycles of sugar feeding. In studies in which the proportion containing nectar sugar was compared with its time of digestion, the high nectar-positive rates and rapid digestion rates suggest that sugar feeding was almost a nightly occurrence (Reisen et al. 1986, O'Meara and Mook 1990).

Competition with blood-host stimuli: Blood-feeding and nectar feeding sometimes may be segregated in time (McCrae et al. 1969, Reisen et al. 1986). But usually these activities overlap broadly, suggesting that they share a nonspecific flight activity period (Yee and Foster 1992, Yee et al. 1992) and are thus in competition. It is generally thought that blood-host stimuli are dominant over simultaneously presented sugar-related stimuli and that the response to sugar sources is less intense, vigorous, or rapid (Christophers 1960). This is to be expected, because blood is probably often more difficult to obtain and more critical to fecundity between reproductive cycles. However, females may prefer fruit stimuli over blood-related stimuli early in adult life (Bowen 1992a). And some species maintained without sugar are unlikely to take blood, even when it is offered alone (Nayar and Sauerman 1975b, Nayar and Pierce 1980). The relative strengths of opposing blood-host and sugar-host stimuli determine the likelihood of a female choosing one or the other (Hancock and Foster, unpublished data), and after a sugar meal, her preference shifts rapidly to blood (Hancock and Foster 1992, 1993b). Changes in a mosquito's energy status probably cause a continuing dynamic interplay between thresholds of response to the 2 kinds of stimuli. Even when continuously exposed to blood-host stimuli in the laboratory, most species continue to feed periodically on fruit-scented sugar (Yee and Foster 1992). But the synanthropic *Aedes aegypti* (Linn.) and *Aedes albopictus* (Skuse) cease sugar feeding in the presence of blood-host stimuli. This fits with the concept of *Ae. aegypti* as a mosquito that preferentially derives its energy from blood alone (Nayar and Sauerman 1971, 1975b; Edman et al. 1992; Scott et al. 1993).

Conclusions: The foregoing suggests that sugar-related attractants may be less powerful than those associated with blood but would nevertheless provide a useful tool in traps for studying or manipulating mosquito populations. This is primarily because sugar is apparently such an important and continuing component of a mosquito's adult life. These attractants draw the same components of a population as do blood-host stimuli, and in addition they attract males, both sexes at an earlier time after emergence, some

females throughout the gonotrophic cycle, and females in reproductive diapause.

VISUAL ATTRACTANTS

It is not known whether mosquitoes use visual cues to locate sugar sources. Several authors have noted that the most commonly used flowers are pale-colored or white (Sandholm and Price 1962; Grimstad and DeFoliart 1974; Magnarelli 1977, 1978, 1979, 1983; Gadawski and Smith 1992). At night, pale objects reflect more light than, and contrast with, the background vegetation, making them easier to locate at low light intensities (Baker 1961). Sandholm and Price (1962) noted a strong mosquito preference for white in such similar and closely related plants as white and red clover. They observed that the darker flowers most often were visited by mosquitoes during full moon on clear nights. Many pale and white flowers are pollinated chiefly by nocturnal insects (Faegri and van der Pijl 1979), and flower nectar flow generally corresponds to pollinator activity periods (Cruden et al. 1983), so perhaps light flowers form the bulk of available nectar sources when nectar-stealing mosquitoes are most active. Also, plants with white flowers are more likely to be fragrant (Percival 1965), enhancing their location at night. But even diurnal mosquitoes seem to favor light flowers (Magnarelli 1977). A contributing factor may be that many colorful flowers have nectaries inaccessible to mosquitoes, being adapted for pollination by long-tongued diurnal nectarivores.

The question of visual cues probably will be best answered by direct experiment. *Aedes aegypti* managed to locate even greatly visually altered flowers, leading Jepson and Healy (1988) to conclude that visual cues alone are not responsible for flower location. Some of the floral parts nevertheless were quite important for attraction, but they presumed that these parts provided olfactory cues.

The exceptions to the rule of light-colored mosquito flowers have been used by some authors to invoke the importance of scent. For example, Grimstad and DeFoliart (1974) noted that despite the similar size and shape of swamp milkweed and common milkweed, only the latter was strongly attractive; it drew more mosquitoes than all lighter-colored hosts combined, apparently compensating for its pink flowers by producing a very strong scent. But Stoutamire (1968) states that the ground orchid *Habenaria*, which is pollinated by mosquitoes and has green flowers that blend with the background, has no detectable scent. McCrae et al. (1969) concluded that mosquito attraction to particular plant species in Africa is so variable and unpredictable that the ac-

cessibility of their nectar seems to be their only commonality. The ability of mosquitoes to locate extrafloral nectaries or honeydew deposits poses an especially intriguing puzzle: in most cases these sugar sources lack strong visual or olfactory cues perceptible to humans.

OLFACTORY ATTRACTANTS

Flower fragrance: Pure sugars have a low vapor pressure and thus provide no volatile gradient or plume from a source, though they can cause aggregation once the mosquitoes make contact. Statements indicating preferential attraction to particular kinds or mixtures of sugars in a flower are referring to either contact chemoreception or an evolved host preference mediated by other stimuli (Grimstad and DeFoliart 1974). However, even small amounts of impurities in cane sugar make it slightly attractive (de Meillon et al. 1967, McCrae et al. 1969).

Field workers report that strongly fragrant flowers have more feeding mosquitoes (Haeger 1955, Sandholm and Price 1962, Grimstad and DeFoliart 1974). Haeger observed that of 2 types of perfect buttonwood flower, the long-stamen type had a more strong and distinct honey odor and was the one usually visited by mosquitoes. Thorsteinson and Brust (1962) demonstrated that only certain flower odors are attractive or arresting, by eliciting aggregations of *Ae. aegypti* on cotton wool above honeys and some kinds of flowers, but not others. McCrae et al. (1969) have cited flowers having strong, sweet scents that apparently are completely unattractive. Raw honey serves as an effective attractant in wind-tunnel olfactometers (D. A. Carlson, unpublished data; Hancock and Foster 1993a); apparently its odor is a combination of fragrances pervading the nectaries of flowers visited by honey bees. And raw fruit attracts mosquitoes in both the laboratory (Bowen 1992a) and field (Reisen et al. 1986).

Extracts: Extracts of plants and plant products have been prepared and tested for their attractiveness, either to facilitate behavioral experiments or to identify attractive components. Thorsteinson and Brust (1962) found that commercially obtained rose extracts caused *Ae. aegypti* to aggregate, but that strawberry and lilac extracts might be repellent. D. A. Carlson (unpublished data) prepared an ether extract of natural honey that in a flight-tunnel olfactometer trapped more than 1/3 of the *Ae. aegypti* males in a 3-min test. An ether extract of honey was used by Wensler (1972) to observe various behavioral aspects of attraction in *Ae. aegypti*; up to 50% of both males and females rapidly formed probing aggregations when the extract was presented outside a screen. Kline et al. (1990) have used a

hexane honey extract successfully as an attractant for *Aedes taeniorhynchus* (Wied.) and *Culex nigripalpus* Theobald in the field. P. L. Davis and J. A. Fluno (unpublished data) prepared an ethanol extract of the climbing milkweed flower *Amphistelma* that was strongly attractive to *Ae. aegypti* on wet paper disks. The ether-soluble fraction of this extract was about 6 times more attractive than the water-soluble fraction. Using chloroform as a solvent, flowers of the same plant were used to prepare an extract that was attractive to both *Ae. aegypti* and *Anopheles quadrimaculatus* Say.

Vargo and Foster (1982) prepared solvent extracts of common milkweed flowers with solvents ranging widely in polarity. Using a probing chamber to quantify responses of *Ae. aegypti* to these extracts, they found no differences in their attractiveness. A comparison of the probing responses of food-deprived *Ae. aegypti* to milkweed, goldenrod, and honey extracts at daily intervals from emergence onward demonstrated the superiority of honey and milkweed as attractants, in agreement with their stronger fragrance and with the infrequent occurrence of mosquitoes on goldenrod in the field when other flowers are accessible (Vargo and Foster, unpublished data). Jepson and Healy (1988) obtained good attraction results with *Ae. aegypti* to ox-eye daisy flowers and certain of their parts in a wind-tunnel olfactometer but failed to produce an attractive solvent extract of them with any of several solvents. However, they obtained an extract of yarrow attractive to *Anopheles arabiensis* Patton (Healy and Jepson 1988), by capturing head-space volatiles with activated charcoal. Other studies have concluded (Williams 1983), and our experience with milkweed confirms, that head-space sampling of flower volatiles on a solid absorbent, rather than solvent extraction, captures the most realistic (to insects and humans) and natural floral odor.

Synthetic fragrances: Synthetic substances prepared commercially by the food and fragrance industries also have been tested for attractiveness. D. A. Carlson (unpublished data) compared 14 imitation flavors in a wind-tunnel olfactometer with *Ae. aegypti* and found imitation cherry and apple particularly attractive. Hancock and Foster (1992), using *Cx. nigripalpus* in a wind-tunnel olfactometer, achieved greater attraction to honey spiked with synthetic apple blossom oil than to honey alone. And contrary to the experience of Thorsteinson and Brust (1962), Yee and Foster (1992) used synthetic strawberry flavoring as an effective attractant for electronic sugar-feeding monitors.

Identification of attractants: Efforts to identify the specific volatile chemicals that attract mos-

quitoes has only just begun. One approach is to analyze and test the components of extracts of plant materials and products. D. A. Carlson (unpublished data) demonstrated the attractiveness of methyl- and ethyl-phenylacetate, major components of honey fragrance, to *Ae. aegypti*. And in a gas chromatograph Healy and Jepson (1988) detected 16 peaks in their attractive yarrow extract, the largest of which was tentatively identified by mass spectrometry as a cyclic or bicyclic monoterpene. Further analysis was not attempted and its attractiveness in isolation was not tested. In our extract of milkweed (Hancock and Foster, unpublished data) the most abundant component was an acyclic monoterpene, (E)- β -ocimene.

A different approach to the identification of mosquito attractants is to screen plant-derived compounds for behavioral or chemosensory activity. Surveys of plant volatiles in general yield a bewildering array of compounds, together comprising the distinctive fragrance. The major categories of plant fragrances ("essential oils") are the aliphatic free acids, alcohols, esters, aldehydes, and ketones; the terpenes; the aromatics (phenols); and miscellaneous nitrogen and sulfur compounds. Among them, those most often responsible for characteristic plant odors are the terpenes and the aliphatic esters and aldehydes (Nicholas 1973a). According to Rodriguez and Levin (1976), the scents specifically of flowers usually consist of the acids; alcohols, aldehydes, and ketones of the terpenes and aromatics; the simple carboxylic acids; the pyrrolizidine and indole alkaloids; the amines; and the glucosinolates. Those most often cited by the time of that writing were the monoterpenes eugenol, linalool, geraniol, and cineole; and the aromatics benzyl alcohol and benzyl acetate. Williams (1983) named many others. The monoterpenes are particularly diverse; surveys indicate that among the higher plants there are 208 acyclic, 400 monocyclic, and 250 bicyclic forms (Nicholas 1973b). But despite analyses of solvent extracts of sunflowers and steam distillates of tansy flowers that have produced 100–200 compounds (Thiery et al. 1990, Gabel et al. 1992), the number of head-space volatiles produced by flowers is not necessarily so daunting. For example, alfalfa flowers produced 33 compounds, the predominant one being the terpene (E)- β -ocimene (Buttery et al. 1982). And the flowers of red clover are reported to produce 2 aliphatic ketones, one aliphatic aldehyde, 6 aliphatic alcohols, one aliphatic ester, 3 terpenes, and 4 aromatics; the major constituents are 2 aromatics: acetophenone (24%) and methylcinnamate (11%) (Buttery et al. 1984).

We are aware of 2 published efforts to screen

some of the above classes of compounds for mosquito responses. Lacher (1967) made extracellular recordings of sense cells associated with the sensilla trichodea types A1, A2, and A3 on the antennae of *Ae. aegypti* females. Among the compounds exposed to the sensilla were 5 acyclic and monocyclic monoterpenes. These had a depressing effect on the spontaneous activity of A1 cells and excitatory or depressing effects on A2 cells, and one compound (citral) had a strongly excitatory effect on an A3 cell. Bowen (1992b) similarly made recordings from the cells associated with A2 sensilla on *Culex pipiens* Linn. females, exposing them to a wide variety of terpenes, green plant volatiles, fatty acid esters, and miscellaneous plant-derived compounds. Of 36 cells surveyed, 19 were relatively specific for bicyclic terpenes containing a ketone group (thujone or verbenone); 4 of these responded to both, and 2 responded to thujone and 4-methylcyclohexanol. The other 17 cells had higher spontaneous activity and were broadly tuned, responding both to the bicyclic terpenes and one of the following: acyclic and monocyclic terpenes, fatty acid esters, green plant odors, or 4-methylcyclohexanol. In all cases the responses were excitatory, and the broadly tuned cells had a greater sensitivity to thujone than the more specific cells. A probing-response assay to thujone demonstrated that it was dependent on both stimulus dose and time of food deprivation. Preliminary attempts at using bicyclic terpenes to elicit an upwind response were unsuccessful.

FLORAL ATTRACTION IN OTHER INSECTS

A useful research shortcut to the identification of mosquito floral attractants might be found in the information on well-known plant-insect pollinator systems. Such an approach would be most effective if mosquitoes are not plant-host specific. Mosquitoes do exhibit preferences among the plants they utilize in one area (Sandholm and Price 1962, Grimstad and DeFoliart 1974, Magnarelli 1977), and in the American tropics there are differences among some mosquito genera in the plant species they utilize, suggesting specialization (Foster, unpublished data). But most reports indicate attraction to a wide variety of flowers. For example, *Aedes vexans* Meigen in Minnesota visited 39 species of plants (Sandholm and Price 1962), suggesting that either it responds to a wide range of chemical stimuli or one or more attractants are produced by a wide range of flowering plant species. Therefore, a knowledge of the major attractants used by other insects to locate flowers might serve as a guide.

Until recently there have been relatively few

studies defining the role of specific flower volatiles in flower-pollinator interactions, or even plant-herbivore ones (Rodriguez and Levin 1976). None of the primary flower volatiles found in alfalfa and red clover (above) was attractive or stimulatory to seed chalcids in behavioral bioassays (Kamm and Buttery 1983, 1986a, 1986b) but many of them elicited strong electroantennogram (EAG) responses (Light et al. 1992), suggesting that more sensitive behavioral methods need to be developed. Simultaneous gas chromatogram (GC) and electroantennogram analysis (coupled GC-EAG) of extracts has proven an efficient method for screening large numbers of flower volatiles for biological activity in insects. Of > 100 volatiles detected in the polar fraction of a solvent extract of sunflowers, only 24 elicited clear EAG responses in honey bees (Thiery et al. 1990), and 6 of these had been shown previously to be recognized by honey bees trained to respond to the total flower aroma (Pham-Delegue et al. 1986). These were bornyl acetate, vanillin, propiovanillone, a branched methyl ester, and 2 unidentified compounds; some of the 10 EAG-active terpenes detected were thought to play a behavioral role as well. A similar coupled GC-EAG study with tansy flowers (Gabel et al. 1992) yielded a steam distillate with 200 GC peaks, 9 of which elicited EAGs in 70% of grapevine moths. All of these compounds were terpenes, the predominant one being β -thujone, and even the very minor ones produced clear EAGs. A synthetic combination of 8 of these terpenes was tested in field cage traps and caught almost as many moths as crude extract. It is not known whether the moth uses this flower as a source of nectar, but mosquitoes do (Andersson and Jaenson 1987, Jaenson and Ameneshewa 1991).

One famous early investigation of the chemical basis of pollinator attractancy and the importance of chemical blends is that of orchids and orchid bees. This revealed about 60 monoterpenes, esters, and alcohols (usually 7-10 per species) making up the major basis of the distinctive fragrance of each orchid species. Single compounds were found to be attractive to many bee species, but the specific mixture of compounds make the fragrance attractive only to specific bees (Hills et al. 1968, 1972; Williams and Dodson 1972). A recent field exploration of the attractiveness of specific mixtures of sunflower floral volatiles to seed weevils was conducted by reconstituting combinations of 5 major components: 4 terpenes and one aliphatic ester or aldehyde. It was found that specific deletions or combinations of deletions decreased the attractiveness of the mixture, and the deviations from the ratio of the natural product also reduced attractiveness (Roseland et al. 1992). These results

emphasize the importance of particular blends of floral volatiles to monophagous insects.

PROSPECTS

Whether particular compounds and blends, apparently so important to host-specific insects, will be important to such generalist nectar thieves as mosquitoes remains to be seen. At least some components of floral odor occur in several plant species and may be useful to generalists. The identification of both narrow-tuned and highly sensitive broadly tuned receptors of plant volatiles (Bowen 1992b) suggests that mosquitoes are designed to discriminate among mixtures, while retaining the option to respond to a variety of blends and individual components. The methods for identifying nectar-related volatiles and screening them for biological activity have reached a stage of sophistication and speed (Patt et al. 1988, Thiery et al. 1990, Charlwood and Charlwood 1991, Light et al. 1992) when it will be possible to make an extensive effort to sort out the likely candidates for further research. Behavioral bioassays of these candidate compounds, by themselves and in various combinations, will be critical to determining their potential for efficacy in the field.

The usefulness of nectar-related attractants in the field remains in doubt. It is now clear that most mosquitoes feed on sugar quite frequently, but this does not guarantee that fragrance-baited trap catches will reflect this. If plant sugars are so abundant and accessible that artificial attractants have difficulty competing with natural ones, higher release rates would not necessarily counter this effect; they might well be repellent at high concentration. Blood-host attractants, on the other hand, may be more effective, both because often there is less competition from natural sources and because the response to them is so vigorous. We know of 2 published reports of the use of plant attractants in traps, and they appear to bear this out. Reisen et al. (1986) made no attempt to compare attractants, but their report is indicative: they captured 150 *Culex tarsalis* Coq. females using 2 melon-baited suction (lightless CDC) traps, but captured 350 in a walk-in resting box over a similar period of time, and far more in a CO₂-baited trap. More promising, Kline et al. (1990) captured a mean of 2,773 *Ae. taeniorhynchus* females per trap-day in honey-extract-baited suction traps, not significantly different than those baited with phenol (1,402), octenol (3,860), and octenol + phenol (5,343), but fewer than those baited with CO₂ (11,700), all of which are blood-host kairomones.

We presume that stronger or more attractive blends of floral attractants can provide propor-

tionately larger field catches. It is already clear that the attraction of nectar-feeding mosquitoes offers qualitative advantages over the attraction of blood feeders, at least for population sampling. Thus, slow release formulations of nectar-host attractants can provide a useful (and also pleasant smelling) alternative or addition to blood-host odors in low-maintenance traps.

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