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The roles of kairomones, synomones and pheromones in the chemically-mediated behaviour of male mosquitoes

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ABSTRACT

Despite decades of intensive study of the chemical ecology of female mosquitoes, relatively little is known about the chemical ecology of males. This short review summarizes the current state of knowledge of the chemicals that mediate male mosquito behaviour. Various trophic interactions including insect–plant, insect–host, and insect–insect responses are emphasized. The relevance of the chemical ecology of male mosquitoes in the context of vector control programmes is discussed.

1. Introduction

Observations regarding the interactions of animals and their chemical environments began in earnest in the late 19th and early 20th centuries, but it was not until the middle of the 20th century that the major concepts of chemical communication and a new vocabulary were introduced by noted researchers Karlson and Lüscher (1959) and Butenandt et al. (1959). Since then, substantial progress has been made in the isolation, identification, and synthesis of chemical compounds and in the confirmation of their activities through bioassays utilizing a variety of animal models. Over the past forty years, the development of analytical techniques like gas chromatography–mass spectrometry (GC–MS), high-performance liquid chromatography (HPLC), solid-phase microextraction (SPME) and electrophysiology have paved the way for a wide range of studies and vast publication record focused on the chemical ecology of insects. The knowledge base produced by these studies has lead directly to the production of novel control strategies for pests in agriculture and forestry (Witzgall et al., 2010). Among the earliest studies of insect chemical ecology was a report published by Willem Rudolfs that established the importance of various stimuli, including chemical compounds, in eliciting changes in mosquito behaviour (Rudolphs, 1922). Rudolfs' use of the term "chemotropism" did not necessarily imply directed movement along a chemical gradient, which is the more modern definition of the behaviour. Instead, he used the term to describe mosquito activation and/or attraction in response to odours (Rudolphs, 1922). Two studies of mosquito responses to floral odours were published in the second half of the 20th century (Sandholm and Price, 1962; Thorsteinson and Brust, 1962; Hancock and Forster, 1982, Healy and Jepson, 1988). Q2 Later, Clements' general textbook on mosquitoes (1999) synthesized several aspects of olfaction, sensory reception and

Abbreviations: GC–MS, gas chromatography–mass spectrometry; HPLC, high-performance liquid chromatography; SPME, solid-phase microextraction; SIT, sterile insect technique; GM, genetically-modified; GLV, green leaf volatiles; GC-EAD, gas chromatographic-electroantennographic detection; DDT, dichlorodiphenyltrichloroethane; DEET, N,N-diethyl-*m*-tolumide; Ors, odourant receptors; Irs, variant ionotropic receptors; Grs, gustatory receptors; Obps, odourant binding proteins.

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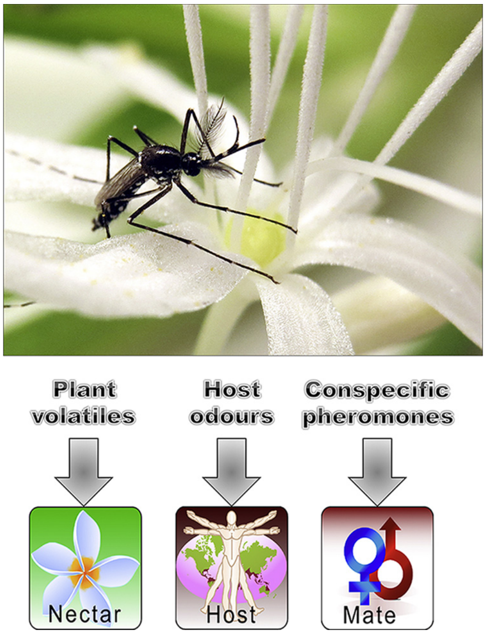

Fig. 1. Male mosquito trophic interactions. Male mosquitoes utilize a variety of volatile and contact chemical cues to orient towards sources of sugar, vertebrate hosts, and conspecifics.

behaviour thus describing the general basis of chemoreception in mosquitoes. In the 21st century, the odour-mediated host interactions of female mosquitoes have been widely investigated, but only recently have other trophic interactions like mosquito–plant interactions been studied. Several reviews have focused on specific aspects of female mosquito ecology, particularly host seeking, and are not discussed here (Takken and Verhulst, 2013; Verhulst et al., 2010; Takken and Knols, 1999; Costantini et al., 1999; Bently and Day, 1989). Importantly, the behaviour of male mosquitoes has been largely ignored and thus there is a significant gap in our knowledge of male chemical ecology. This short review is intended to provide a summary of our current knowledge of the chemical ecology of adult male mosquitoes based upon various trophic interactions that have been described in scholarly publications: insect–plant (kairomones and synomones involved in nectar feeding), insect–insect (pheromones mediating male–female interactions), and insect–host (kairomones attracting species that mate near hosts). Studies that focus on male mosquitoes, which have paled in comparison with the numbers of studies focused on females, will not only enhance our understanding of basic mosquito biology, but are likely to directly impact vector control or surveillance. Specifically, we expect that integrated control strategies which utilize mass releases of laboratory-reared species, either in the context of the sterile insect technique (SIT) or in the use of genetically-modified (GM) mosquitoes, will benefit from a deeper understanding of the chemical ecology of male mosquitoes.

2. Sources of the semiochemicals involved in male mosquito behaviour

As shown in Fig. 1, at least three chemically-mediated behaviours have been observed in male mosquitoes: the search of food sources (insect–plant), the search for hosts where conspecific females are likely to be found (insect–host), and the selection of sexual partners (insect–insect). With respect to communication level, i.e. to which species message sending and receiving individuals belong to, the relevant semiochemicals involved in each of these behaviours can thus be considered as falling into two categories: the allelochemicals (kairomones, and synomones), which mediate interspecific interactions, and the pheromones, which mediate intraspecific interactions (Whittaker and Feeny, 1971). Kairomones are volatile compounds emitted by one species that are beneficial to the receiver. These compounds are involved in the mosquito–plant and mosquito–host interactions. In the first case, kairomones are produced by flowers, leaves or fruits and attract both sexes towards nectar sources, or perhaps resting sites. In the second case, kairomones are produced by humans or animals as breath, sweat, or skin emanations and attract female mosquitoes towards sources of blood-feeding. These same kairomones may be utilized by males of some species for attraction to hosts for mate location. Carbon dioxide is the most common kairomone and often acts synergistically with other compounds to elicit female flight and/or attraction (Gillies, 1980; Kline et al., 1991; Cork, 1996; Takken and Knols, 1999). With respect to pheromones, there are several types of behaviourally active compounds described in insects, but in mosquitoes may include sex pheromones (Kliewer et al., 1966; Nijhout and Craig, 1971; Lang and Foster, 1976; see discussion below) and oviposition pheromones (Osgood, 1971; Starratt and Osgood, 1972; Bruno and Laurence, 1979), both classes having been recognized in various mosquito species. The fatty acid lactone, erythro-6-acetoxy-5-hexadecanolide, is produced and released by ovipositing *Culex quinquefasciatus* females and significantly enhances oviposition by other gravid conspecifics both in the laboratory (Bruno and Laurence, 1979; Laurence and Pickett, 1985) and in the field (Otieno et al., 1988). Without respect to communication level (i.e. odour source), semiochemicals can be also be classified more broadly as attractants, repellents, stimulants, deterrents and arrestants. The repellent properties of many compounds against female mosquitoes have been widely documented and their use as personal protection against blood feeding has been consistently investigated and developed (Debboun and Strickman, 2013). To our knowledge there are only a few publications dealing with the repellent properties of synthetic compounds against male mosquitoes, which will be briefly discussed.

3. Male responses to plant volatiles

Allelochemicals used by mosquitoes to locate food sources fall into two categories: (i) synomones which benefit both odour releasing and perceiving organisms, i.e. plants are pollinated and mosquitoes receive a nectar reward, and (ii) kairomones when only mosquitoes benefit from perceiving the plant signal and taking nectar from flowers without pollinating them. Despite the fact that odour-mediated sugar source seeking in mosquitoes is well documented the chemical identification of plant attractants is rather limited. Data about carbohydrate source location by mosquitoes obtained under field and laboratory conditions indicates that males and females show comparably similar responses and preferences (Jepson and Healy, 1988; Healy and Jepson, 1988; Jhumur et al., 2006, 2007a,b; Otienoburu et al., 2012); electroantennographic responses to floral odours of both sexes were also found to be similar (Jhumur et al., 2007a,b) (Fig. 2).

Electrophysiological recordings revealed a high proportion of both broadly- and narrowly-tuned antennal receptor neurons of *Culex pipiens pipiens* L. sensitive to monoterpenes including thujone, verbenone, α-pinene, limonene, citral, and nerol, to sesquiterpene farnesol as well as three of each green leaf volatiles (GLVs) and fatty acid esters (Bowen, 1992). Behavioural tests showed that bicyclic terpene, thujone, at stimulus intensities within the dynamic range of the terpene-specific Ors, stimulated dose-dependent post-landing feeding responses [probing] in food-deprived, non-bloodfed female mosquitoes. In another study, gas chromatographic-electroantennographic detection (GC-EAD)

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