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Exploiting the chemical ecology of mosquito oviposition behavior in mosquito surveillance and control: a review

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ABSTRACT: Vector control is an important component of the interventions aimed at mosquito-borne disease control. Current and future mosquito control strategies are likely to rely largely on the understanding of the behavior of the vector, by exploiting mosquito biology and behavior, while using cost-effective, carefully timed larvicidal and high-impact, low-volume adulticidal applications. Here we review the knowledge on the ecology of mosquito oviposition behavior with emphasis on the potential role of infochemicals in surveillance and control of mosquito-borne diseases. A search of PubMed, Embase, Web of Science, Global Health Archive, and Google Scholar databases was conducted using the keywords mosquito, infochemical, pheromone, kairomone, allomone, synomone, apneumone, attractant, host-seeking, and oviposition. Articles in English from 1974 to 2019 were reviewed to gain comprehensive understanding of current knowledge on infochemicals in mosquito resource-searching behavior. Oviposition of many mosquito species is mediated by infochemicals that comprise pheromones, kairomones, synomones, allomones, and apneumones. The novel putative infochemicals that mediate oviposition in the mosquito subfamilies Anophelinae and Culicinae were identified. The role of infochemicals in surveillance and control of these and other mosquito tribes is discussed with respect to origin of the chemical cues and how these affect gravid mosquitoes. Oviposition attractants and deterrents can potentially be used for manipulation of mosquito behavior by making protected resources unsuitable for mosquitoes (push) while luring them towards attractive sources (pull). In this review, strategies of targeting breeding sites with environmentally friendly larvicides with the aim to develop appropriate trap-and-kill techniques are discussed. ***Journal of Vector Ecology*** **45 (2): 155-179. 2020.**

Keyword Index: Culicidae, oviposition, infochemicals, olfactory cues, mosquito behavior, surveillance, control.

INTRODUCTION

Exploring the chemical ecology of oviposition behavior in mosquitoes may lead to the ecological understanding of the origin, role, and significance of natural organic compounds mediating various interactions within and between mosquito species and their surroundings. The observation of such interactions in nature and the elucidation of compounds involved may contribute to the development of novel control and surveillance strategies necessary for the management of mosquitoes and mosquito-borne diseases. Most of the existing mosquito control strategies interfere with mosquito behaviors, especially biting and resting (Pates and Curtis 2005).

The need to develop new vector control methods and improve implementation of existing ones has led to the exploration of interactions in the oviposition phase of mosquitoes in an attempt to understand the mechanism of interactions and elucidate the structures of the chemical compounds regulating oviposition behavior. A control strategy that deploys chemicals attracting/stimulating or deterring gravid females intending to oviposit is considered to be novel. It would contribute to addressing the global demand for the reduction of toxic chemicals in the environment and therefore could be an essential component of integrated vector management strategies in the future (Cook et al. 2006).

Many mosquito species exhibit oviposition behavior through specific selection of larval sites (Osgood 1971, Laurence et al. 1985, Blackwell et al. 1993, Chadee et al. 1993 et al., Zahiri et al. 1997, Allan and Kline 1998). Generally, mosquitoes avoid ovipositing in sites that are occupied by competitors or predators (Kiflawi et al. 2003a, Blaustein et al. 2004). They tend to oviposit in habitats with conspecific larvae, as these indicate the suitability of the habitat for the survival of the next generation (Blaustein and Kotler 1993, Allan and Kline 1998, Mwingira et al. 2019). Therefore, mosquitoes are discriminating in selecting sites for oviposition, as they occupy a non-random set of aquatic habitats (Heard 1994, Minakawa et al. 2004).

Biotopes occupied by the immature stages are sites selected by their mothers (Clements 1992, Mwingira et al. 2009, Mwingira et al. 2019). Consequently, oviposition-site selection can influence the distribution and dynamics of the next generation (Spencer et al. 2002). Thus, female mosquitoes can increase their contribution to the next generation by selecting oviposition sites without predators and competitors (Kiflawi et al. 2003b, Blaustein et al. 2004) or with abundant food (Blaustein and Kotler 1993, Sherratt and Church 1994).

Oviposition-site selection by mosquitoes is a critical factor for fitness and is therefore an essential part of the life-history of all species (McCall and Cameron 1995). Understanding insect oviposition decisions may provide further insight into the factors affecting population dynamics and the epidemiology of mosquito-borne diseases and assist in predicting population responses to control measures (Nylin 2001, Pates and Curtis 2005, Vonesh and Blaustein 2010). As only few breeding sites are of epidemiological significance (Keating et al. 2004, Fillinger et al. 2009), investigating the site-selection behavioral process of female mosquitoes in an attempt to develop a control strategy is crucial.

Previous studies on oviposition-site selection of mosquitoes indicate that many species are capable of using tactile, taste, olfactory, and visual cues to assess such site characteristics as color, reflectance, texture, moisture, salinity, surrounding vegetation, bacterial growth, fungal infusion, conspecific population density, and the presence of a variety of chemicals (Millar et al. 1992, Blackwell et al. 1993, Takken and Knols 1999, Sivagnaname et al. 2001, Saveer et al. 2018). Several studies have confirmed the mediation of oviposition behavior in mosquitoes by intra- and inter-specific chemical signals across different species (Afify and Galizia 2015). Most of these findings came from the Culicinae subfamily, which has been the mosquito group most intensively studied. The objective of this review is to explore the role of infochemicals in mediating oviposition behavior of mosquitoes and evaluate how these cues may be used for mosquito control.

PHYSICAL STIMULI

Many studies have explored possible roles of visual, tactile, olfactory, and taste stimuli in mediating oviposition behavior in mosquitoes (Beehler et al. 1993, Reiskind and Zarrabi 2012). The function of the senses of mosquitoes is summarized by Montell and Zwiebel (2016).

Visual cues

The major sense organs of most insects include compound eyes, simple eyes, and antennae. Stemmata are the simple eyes found in mosquito larvae. The structure of the eye varies depending on whether the insect is habitually active only by day or by night. Vision is most widely used by diurnal insects, which live in open habitats (Lehane 2005). In many nocturnal and semi-nocturnal insects, the eye is large enough to allow maximum photon capture, and contrast sensitivity is improved at low ambient light levels (Land 1981). Groups of facets in different parts of the eye may vary for different kinds of vision; for example, separate groups of facets may have specialized sensitivity to color and light. This is illustrated by the relationship between theoretical optimum eye parameters and various illuminance conditions as observed for *Aedes aegypti* (Muir et al. 1992).

Most mosquitoes have apposition eyes, which do not function well at low light intensities (Clements 1999). However, *Anopheles gambiae* have exceptional, conically-shaped eyes that allow photons to be intercepted by the lens (Land et al. 1997). Their apposition eye is adapted for high sensitivity in dim environments, where high photon capture takes precedence over fine resolution (Kirschfeld 1974). Therefore, *An. gambiae* appears to be more sensitive to light intensity than other mosquito species (Land et al.1999).

Most mosquito species are capable of discriminating wavelengths of various ranges during oviposition. For *Aedes aegypti*, oviposition-site acceptability is negatively correlated with intensity of illumination (Clements 1999). Oviposition water treated with a colored dye has been reported to be more attractive to gravid *Ae. triseriatus* and *Cx. quinquefasciatus* than untreated water (Williams 1962). Black- and red-colored containers are preferred for oviposition by *Cx. annulirostris* and *Cx. molestus,* respectively (Dhileepan 1997).

Similarly, *Toxorynchites amboinensis* and *T. moctezuma* oviposit preferentially into black containers rather than white, yellow, green, or blue (Collins and Blackwell 2000). Black ovitraps are the most preferred target for gravid *Ae. albopictus* seeking artificial oviposition sites (Hoel et al. 2011). Black substrates have been reported to elicit most oviposition by both laboratory and house-collected *An. gambiae* mosquitoes (Huang et al. 2006, Huang et al. 2007). In general, the majority of mosquito species prefer a black-colored, followed by blue-colored, oviposition background.

Tactile cues

Despite the fact that antennae are the chief site of the sense of touch in insects, the entire insect body is covered by a variety of tactile bristles, scales, and pits that are used for detecting cues through physical contact. The touch receptors of the antennae are the fine hair-like bristles with which they are covered. Tactile cues are important stimuli in the activation and orientation of many blood-sucking insects (Allan et al. 1987). Taste organs occur not only on the mouth parts but also on the antennae, palpi, tarsi, and egg-laying appendages. Unlike visual stimuli, which are important signals when the insect is still at some distance from an oviposition site, heat and moisture become important when the insect is near an oviposition site (Lehane 2005, Okal et al. 2013, Spitzen and Takken 2018).

Gravid mosquitoes often touch the water using either mouthparts or legs before the onset of oviposition. Taste as a mode of infochemical reception has been observed clearly in *Ae. albopictus* and *Ae. triseriatus,* where oviposition responses were mediated by contact chemostimulants rather than attraction to odorants (Trexler et al. 1998). Therefore, for a better understanding of infochemical perception by mosquitoes during oviposition, it is important to separate physical from odorant reception of cues (Sumba et al. 2004, Mwingira et al. 2019).

Moisture and temperature

The antennae of most insects also bear receptors sensitive to moisture content in the air and to temperature. Moisture content in the air was identified as one of the most important variables explaining the dynamics of oviposition, given the need for moist landscapes in which mosquitoes may search for oviposition sites (Day et al. 1990, Edman et al. 1998). On the other hand, there is a strong positive correlation between soil moisture content, quantified as surface conductivity and the degree of oviposition activity, which peak at saturation with standing water (Koenraadt et al. 2003, Huang et al. 2006, Saifur et al. 2010).

Temperature increases contribute to the rise of water vapor in the vicinity of potential larval habitats and therefore, influences the ability of gravid mosquitoes to locate those sites (Okal et al. 2013). Environmental factors including temperature, humidity, and air pressure are significantly correlated with the oviposition of *Culex pervigilans* (Zuharah and Lester 2010). Water vapor is, therefore, a long-range cue and once close to the oviposition site, the insects detect other cues through tactile and taste receptors (Amarakoon et al. 2008).

CHEMICAL STIMULI

Infochemicals influencing oviposition behavior

Insect resource-seeking processes are mediated through chemical senses. Insects use infochemicals from their environment at all stages of development to locate food, oviposition, and hibernation sites, to come together with conspecifics and sexual partners, and to avoid dangerous situations or unsuitable habitats and hosts (Agelopoulos et al. 1999). Olfaction and taste are employed in recognizing infochemicals by insects (Lewis 1984, Montell and Zwiebel 2016). Some of the earliest examples of infochemical-mediated activities reported for mosquitoes are summarized in Table 1.

When searching for potential oviposition sites, mosquitoes are guided by long-range infochemicals such as pheromones to identify their presence (Pickett and Woodcock 1996, Okal et al. 2013). When close to the site, the mosquito uses short-range infochemicals to discriminate between a suitable and unsuitable breeding site for their next generation. At an oviposition site, infochemicals play a crucial role in the gravid female's assessment of chemical properties of the prospective habitats for the immature stages (Takken and Knols 1999). Mosquitoes use contact stimuli to evaluate water quality and other factors prior to oviposition (Bentley and Day 1989).

Mechanisms of odor reception and signal transduction

Insects have small cuticular extensions of various forms, called sensilla, which are involved in stimulus perception and can be found on various parts of the body, including the head and legs (McIver 1982, Hansson and Hallberg 1999, Hansson and Stensmyr 2011). Due to the widespread presence of olfactory cues in their environment, insects have a highly sensitive and specific system of odor discrimination (Carey and Carlson 2011). They can find their resources precisely, despite being exposed to complex odor profiles from various sources (Hansson and Anton 2000, Zwiebel and Takken 2004). Insects detect odors by means of olfactory receptor neurons (ORNs) (Carey et al. 2010) housed in the sensilla, which are odorant-specific as they are expressed by individual odorant receptor genes (Su et al. 2009). A standard insect olfactory sensillum contains one to several bipolar ORNs that send their sensory dendrites into the sensillum lumen.

Mosquitoes have several types of olfactory sensilla. These include sensilla trichodea, grooved peg sensilla, capitate peg sensilla, and coeloconic sensilla, which they use as infochemical receptors. The genes encoding expression of various classes of these organs are regulated depending on the timing of a specific activity within the gonotrophic cycle. For example, after ingestion of a blood meal, the mosquito stops host-seeking, as receptors of oviposition cues become more sensitive to stimuli used in the search for an oviposition site. Host-seeking behavior is restored again 24 h after oviposition (Klowden and Lea 1979a,b, Takken et al. 2001). Furthermore, it has been reported that blood feeding results in the activation of a new functional class of trichoid sensilla, which is not usually expressed in mosquitoes that have never had a blood meal (Qiu et al. 2006). Apparently, several chemicals activate this sensillum (Table 2), indicating that they are putative infochemicals mediating oviposition behavior in mosquitoes (Liu et al. 2018). Some of these chemicals have already been shown to mediate oviposition behavior in mosquitoes through behavioral assays (Eneh et al. 2016b, Gaburro et al. 2018). Such compounds are 3-methylindole, 2-ethylphenol, 4-ethylphenol, and 4-methylphenol (Table 3).

PRINCIPAL OVIPOSITION CHEMICAL SIGNALS

Infochemicals were originally classified according to the origin of the compounds in specific interactions. However, the classification was ambiguous, because in reality the producer or emitter may be a different organism from the same or even at another trophic level, being associated to at least one of the interactants (Dicke and Sabelis 1988). Consequently, the discussion on classification of mosquito infochemicals is based on cost-benefit analysis criteria. An infochemical is therefore defined as a chemical that conveys information that mediates an interaction between two individuals by evoking physiological and/or behavioral responses that benefit the emitter, receiver, or both (Dicke and Sabelis 1992). Several infochemicals have been described and are discussed below.

Allelochemicals

Mosquitoes interact with organisms outside their species mainly through allelochemicals. These are infochemicals that mediate interactions between two individuals of different species. They are grouped into the following classes: kairomones, allomones, and synomones.

Kairomones

A kairomone evokes a behavioral or physiological response that benefits the receiver but not the emitter (Dicke and Sabelis 1988). Owing to their ability to assist insects/predators to locate their hosts, kairomones have been exploited to develop control and surveillance systems for host-seeking insects (Dicke et al. 1990). The development of traps which use infochemicals such as carbon dioxide (CO_2), lactic acid, ammonia, carboxylic acids, and 1-octen-3-ol to trap host-seeking insects resulted from the exploitation of a kairomonal behavioral response (Kline et al. 1990, Kline et al. 1994, Becker et al. 1995, Kline and Mann 1998, Gibson and Torr 1999, Rueda and Gardner 2003). In their oviposition phase, kairomones play a big role in assisting gravid females to locate suitable breeding sites. The known kairomones mediating oviposition behavior are mainly produced by aquatic plants and algae and the receiver (mosquito) benefits

Table 1. Principal behaviors in mosquitoes that are mediated by infochemicals.

Process	**Infochemicals**	**Signal source(s)**	**Effect(s) of the signal**	**Species**	**Reference**
Mating	Pheromones	Conspecifics	To bring both sexes together	*Mansonia* spp.	McIver et al. 1980
Plant feeding	Synomones	Fruits, floral nectar & plant spp	To inform mosquitoes about the presence of food	*An. gambiae*	Foster & Hancock 1994 Foster & Takken 2004 Impoinvil et al. 2004 Nyasembe et al. 2012, 2014
				An. sergentii	Junnila et al. 2010
				Ae. aegypti	Healy & Jepson 1988 Martinez-Ibarra et al. 1997
				Cx. nigripalus	Hancock & Foster 1997
				Cx. pipiens	Jhumur et al. 2006, 2007, 2008 Otienoburu et al. 2012 Bowen et al. 1992
Host-seeking	Kairomones	Vertebrates	To inform mosquitoes about the presence of food	*An. albimanus*	Knols et al. 1994
				An. gambiae	Smallegange et al. 2005 Njiru et al. 2006 Mweresa et al. 2016
				Ae. aegypti	Williams et al. 2006 Bernier et al. 2007
				Ae. albopictus	Xie et al. 2019
				Culex spp.	Takken et al. 1999 Smallegange et al. 2010 Tian et al. 2018
	Allomones	Vertebrates	To mask attractiveness of hosts to mosquitoes	*An. gambiae*	Brady et al. 1997 Mukabana et al. 2004
Oviposition	Allomones	Fungi, predators	To induce mosquitoes to oviposit	*Cx. quinquefasciatus*	Mboera et al. 1999
				Aedes spp.	Allan & Kline 1998
	Apneumones	Hay infusion		*Cx. quinquefasciatus*	Millar et al. 1992
	Kairomones	Plants		*An. albimanus*	Torres-Estrada et al. 2005
				An. arabiensis	Wondwosen et al. 2016
				An. arabiensis	Asmare et al. 2017
				An. coluzzii	Asmare et al. 2017
	Pheromones	Egg rafts, larvae	To induce mosquitoes to oviposit	*Cx. quinquefasciatus*	Mboera et al. 1999
				Aedes spp.	Allan & Kline 1998
				An. coluzzii	Mwingira et al. 2019
	Synonomes	Microorganism		*Ae. aegypti*	Melo et al. 2020
				An. gambiae	Sumba et al. 2004 Lindh et al. 2005, 2008 Eneh et al. 2016a

Table 2. Response spectra of ORN innervating sensilla trichodea, grooved peg, and capitate pegs of mosquitoes in relation to oviposition stimulus.

Stimulus	Mosquito species	Response	Sensillum	References
Ammonia and Amines				
Ammonia*	*An. gambiae*	+	ST	Braks et al. 2001, Smallegange et al. 2005
		+	GP	
1-Pentylamine***		+	ST	Qiu et al. 2005
		+	GP	
Carboxylic acids				
3-Methylbutanoic acid*	*An. gambiae*	+	ST	Qiu 2005
		+/–	GP	
Pentanoic acid*		+	ST	Qiu 2005
		+/–	GP	
Hexanoic acid*		+	ST	Qiu 2005; Smallegange et al. 2002
		+/–	GP	
Heptanoic acid**		+	ST	Qiu 2005
Octanoic acid***		+	ST	
Nonanoic acid**		+	ST	
		–	GP	
7-Octanoic acid*		+	ST	Qiu, 2005; Constantini et al. 2002
2-Methyl-2-hexenoic acid*		+	ST	
Alcohol and heterocyclics				
1-Hexen-3-ol*	*An. gambiae*	+	ST	Qiu et al. 2005
2-Phenoxyethanol***		+	ST	
Phenol*		+	ST	
2-Methylphenol*		+	ST	
4-Methylphenol*		+	ST	
4-Methylphenol	*Ae. aegypti*	+	ST	Bentley et al. 1982
4-Ethylphenol*	*An. gambiae*	+	ST	Qiu et al. 2005
4-Methylcyclohexanol	*Ae. aegypti*	+/–	ST, SB, SP	Bentley et al. 1982
	Cx. tarsalis	+/–		
	Cx. pipiens	+/–	ST_2	Bowen et al. 1992
	An. stephensi	+/–		Bentley et al. 1982
Indole**	*Ae. aegypti*	+	ST	Qiu et al. 2005
		+/–	CP	Lu et al. 2007
3-Methylindole***		+/–	ST	Qiu et al. 2005
		+/–	CP	Lu et al. 2007
Geosmin		+		Melo et al. 2020
Ketones				
Butanone***	*An. gambiae*	+/–	ST	Qiu et al., 2005
6-Methyl-5-hepten-2-one*		+	ST	
2-Nonanone***		–	ST	
Geranyl acetone***		–	ST	
Others				
Heptanal***	*An. gambiae*	+	ST	Qiu et al. 2005
Water vapour	*Ae. aegypti*	+	GP	Kellogg et al. 1970
Oviposition site related	*Ae. aegypti*	+/–	GP	David and Sokolove 1976
Oviposition site related	*Ae. aegypti*	+	ST_2	Davis et al. 1976
Oviposition site related	*Ae. aegypti*	+/–	GP & ST_2	Davis et al. 1976
Terpenes	*Cx. pipiens*	+	ST_2	Bowen et al. 1992
Green plant volatiles		+	ST_2	
Fatty acid esters		+	ST_2	

Key: + represents excitation (attraction), – inhibition (deterrence), +/– excitation & inhibition.
ST - Sensilla trichodea, GP - Grooved peg, CP – Capitate peg, Sb - short blunt, Sp - short pointed.
* represents excitation response that occurs before and after blood feeding.
** represents excitation response that increases relatively after blood feeding.
*** represents excitation response that occurs only after blood feeding.

Table 3. Response of gravid mosquitoes to infochemicals mediating oviposition behavior.

Chemical compound	Response(s)	Mosquito species	References
Alcohol/cyclics			
Phenol	0	*Cx. quinquefasciatus*	Millar et al. 1992
4-ethylphenol	0	*Cx. quinquefasciatus*	Millar et al. 1992
	+	*Cx. quinquefasciatus*	Zhu et al. 2013
2-methylphenol	+	*Tx. moctezuma, Tx. amboinensis*	Collins and Blackwell 2002
3-methylphenol	+	*Tx. moctezuma, Tx. amboinensis*	Collins and Blackwell 2002
4-methylphenol	+	*Ae. triseriatus*	Bentley et al. 1981
	0	*Cx. quinquefasciatus*	Millar et al. 1992
	+	*Cx. quinquefasciatus*	Zhu et al. 2013
	–	*Ae. albopictus*	Trexler et al. 2003
	+	*Tx. brevipalpis, Tx. splendens*	Linley et al. 1989
	+	*Tx. moctezuma, Tx. amboinensis*	Collins and Blackwell 2002
4-methylcyclohexanol	+	*Ae. triseriatus*	Bentley et al. 1981
	+	*Tx. moctezuma, Tx. amboinensis*	Collins and Blackwell 2002
Indole	0	*Cx. quinquefasciatus*	Millar et al. 1992
	0	*Ae. albopictus*	Trexler et al. 2003
	0	*Ae. albopictus*	Trexler et al. 2003
3-methylindole	+	*Cx. tarsalis, Cx. stigmatosoma*	Beehler et al. 1993, 1994
	+	*Cx. quinquefasciatus*	Blackwell et al. 1993, Seenivasagan et al. 2013
	–	*Ae. albopictus*	Trexler et al. 2003
	+	*Tx. brevipalpis*	Linley et al. 1989
	+	*Tx. amboinensis, Tx.moctezuma*	Collins and Blackwell 2002
	0	*Tx. splendens*	Linley et al. 1989
Cedrol	+	*An. gambiae, An. arabiensis*	Eneh et al. 2016b
Geosmin	+	*Ae. aegypti*	Melo et al. 2020
Carboxylic acids			
(Z)-9-hexedecenoic acid	+	*Ae. aegypti*	Kumaran et al. 2006
Decanoic acid	+	*Ae. aegypti*	Kumaran et al. 2006
Nonanoic acid	–	*Ae. aegypti, Cx. tarsalis, Cx. quinquefasciatus*	Schultz et al. 1982
Oleic[(Z)-9-octadecenoic] acid	–	*Cx. quinquefasciatus*	Hwang et al. 1983
Butyric acid	–	*Cx. quinquefasciatus*	Hwang et al. 1979
Octanoic acid	–	*Ae. aegypti, Cx. tarsalis, Cx. quinquefasciatus*	Schultz et al. 1982
Fatty acid esters			
Aryl hydrozono	+	*Ae. albopictus*	Bandyopadhyay 2011
	+	*Ae. aegypti*	Guha et al. 2012
Decyl undecanoate	+	*An. stephensi*	Sharma et al. 2009
Heptadecyl butanoate	–	*An. stephensi*	Sharma et al. 2009
Hexadecyl pentanoate	–	*Ae. aegypti, Ae. albopictus*	Sharma et al. 2008
	–	*An. stephensi*	Sharma et al. 2009
Nonyl dodecanoate	+	*An. stephensi*	Sharma et al. 2009
Octyl tridecanoate	+	*Cx. quinquefasciatus*	Seenivasagan et al. 2013
Octadecyl propanoate	–	*An. stephensi*	Sharma et al. 2009
Pentyl hexadecanoate	+	*An. stephensi*	Sharma et al. 2009
Propyl octadecanoate	+	*An. stephensi*	Sharma et al. 2009, Seenivasagan et al. 2012
	+	*Ae. aegypti*	Sharma et al. 2008
	+	*Cx. quinquefasciatus*	Seenivasagan et al. 2013
Tetradecyl heptanoate	–	*Ae. aegypti, Ae. albopictus*	Sharma et al. 2008
	–	*An. stephensi*	Sharma et al. 2009
Tridecyl octanoate	–	*Ae. aegypti, Ae. albopictus*	Sharma et al. 2008
Other chemicals			
Dimethyl disulphide	0	*Ae. albopictus*	Trexler et al. 2003
Trimethylamine	0	*Ae. albopictus*	Trexler et al. 2003

Key: + represents attracting, –: deterring, 0: no response
Ae. – Aedes; *An. – Anopheles*; *Cx. – Culex*; *Tx. - Toxorhynchites*

while the emitters (plants/algae) do not.

There is a positive correlation between mosquito larvae and plants that are present in larval habitats. Various plants are associated with immature stages of mosquitoes. A strong positive association has been observed among larvae of *An. albimanus* and specific vegetation forms, including: *Brachiaria mutica*, *Cynodon dactylon*, *Jouvea straminea*, *Fimbristylis spadicea,* and *Ceratophyllum dermersum* (Rodriguez et al. 1993, Hernandez et al. 1997, Torres-Estrada et al. 2005). Also, the presence and density of *An. farauti* larvae was positively associated with aquatic emergent plants (Bugoro et al. 2011).

In addition to the specific plants that have been observed to play a role in guiding oviposition site selection of mosquitoes, the extracts, such as vegetable dye, from certain green plants have also been found to guide gravid *Ae. triseriatus* (Beehler and DeFoliart 1990). This suggests that a gravid female may be using cues from these plants to select suitable oviposition sites. A mixture of terpenoid and alcohol compounds identified through GC-MS analysis has been found to mediate *Anopheles* oviposition (Rejmankova et al. 2005, Torres-Estrada et al. 2005).

Grass infusions have been shown to contain oviposition stimuli for culicine mosquitoes, including *Ae. albopictus* (Allan and Kline 1995), *Ae. aegypti* (Chadee 1993b), *Ae. triseriatus* (Holck et al. 1988), *Cx. pipiens*, *Cx. restuans* (Reiter 1986, Jackson et al. 2005), *Cx. tarsalis* (Reisen and Meyer 1990), and *Cx. quinquefasciatus* (Millar et al. 1992, Mboera et al. 1999). Consequently, a number of infochemicals, mainly kairomones, have been identified from grass infusions. The attractive compounds include, among others, phenol, 4-methylindole, 4-ethylphenol, 3-methylindole, 4-methylphenol, and indole (Bentley et al. 1981, Millar et al. 1992, Du and Millar 1999). Two compounds in particular, 3-methyl-indole (skatole) and 4-methylphenol (*p*-cresol), have been investigated in more detail (Mboera et al. 2000b). Gravid females of *Cx. quinquefasciatus* had a higher electrophysiological sensitivity for skatole (3-methyl-indole) than males (Blackwell et al. 1993).

A positive correlation between the presence of filamentous algae and the number of mosquito larvae has been well documented (Kramer 1989, Vazquez-Martinez 2002, Torres-Estrada et al. 2007). The presence of certain algal species is the main characteristic in mosquito larval habitats (Savage et al. 1990, Fernandez-Salas et al. 1994, Manguin et al. 1996b), and larval productivity was low in the absence of algae (Rejmankova et al. 1992, Manguin et al. 1996a). Some of the algal species that are associated with mosquito breeding sites are *Spirogyra* spp., *Chladophora* spp., *Oedogonium* spp., and *Closterium* spp., (Fernandez-Salas et al. 1994). In this association, mosquito larvae benefit by feeding on a diet consisting of algae (Gimnig et al. 2002). Filamentous algae *Spirogyra majuscula* and *Cladophora glomerata* were found to represent 47% of the gut content of *An. pseudopectipennis* (Bond et al. 2005). Similarly, phylogenetic analysis of the gut contents from *An. gambiae* larvae revealed that 50% consisted of green algae of the Chlamydomonales and Chlorococcales families (Garros et al. 2008). Volatile compounds released by algae are likely to be the main short-range attractants for gravid mosquitoes. For example, ethyl acetate and higher alkanes (docosane, tricosane, tetracosane, pentacosane, hexacosane, heptacosane, and octacosane) were identified as infochemicals originating from *S. majuscula* and mediate the oviposition behavior of *An. pseudopectipennis* (Torres-Estrada et al. 2007).

Allomones

Allomones are allelochemicals that evoke a behavioral or physiological response that benefits the emitter but not the recipient (Dicke and Sabelis 1988). They are of significant importance in the biological methods of vector control. Allomones of interest in mosquito oviposition behavior are mainly emitted by natural enemies of mosquitoes, such as fungi and aquatic animals.

The association between mosquitoes and fungi has been reviewed in detail with much of the attention being directed to entomopathogenic fungi (Scholte et al. 2004). Several species of entomopathogenic fungi are known to infect mosquitoes successfully, using mosquito bodies for their propagation and dispersal (Scholte et al. 2005). It is not suprising that some fungal infusions attract ovipositing mosquitoes. For example, breeding water treated with aqueous *Polyporus* spp. infusions received significantly more eggs of mosquitoes than other substrates (Sivagnaname et al. 2001). Cedrol is an infochemical emitted by fungi that are living in rhizomes of the grass *Cyperus rotundus* and attracts both *An. gambiae* and *An. arabiensis* (Eneh et al. 2016a). The release of infochemicals that attract mosquitoes to lay eggs in infected sites may be a strategy for the benefit of the fungi.

Certain aquatic animals have been associated with the mediation of oviposition behavior in mosquitoes. Crustaceans and some mollusc species have been investigated for candidate oviposition attractants of mosquitoes. The copepod species *Mesocyclops longisetus*, which previously was used for the biological control of mosquitoes (Calliari et al. 2003), has been found to attract gravid *Ae. aegypti*. These crustaceans release various chemical compounds such as: 3-carene, α-terpinene, α-copaene, α-cedrene, and δ-cadinene that mediate oviposition behavior in mosquitoes (Torres-Estrada et al. 2001). Moreover, water that had been conditioned with carpet shells (*Paphia undulate*) and giant tiger prawns (*Penaeus monodon*) has been found to be highly attractive to gravid *Ae. albopictus* (Thavara et al. 2004). It is plausible for these organisms to attract ovipositing mosquitoes so that they can eat their larvae.

Synomones

Synomones are allelochemicals that evoke a behavioral or physiological response that benefits both the emitter and receiver (Dicke and Sabelis 1988). Synomones affecting oviposition behavior are produced by bacteria that are present in soil, water, plants and fermenting organic matter and attract mosquitoes to lay eggs. Mosquitoes rely on their gut microbes for rapid growth and development (Coon et al. 2014). Consequently, gravid female mosquitoes use volatiles of bacterial origin to assess nutrient availability and durability of habitats, both of which are vital determinants for the survival of their offspring, and hence their fitness (Sumba et al. 2004). On the other hand, bacteria benefit from mosquito site-selection behavior as they feed on food processed by mosquito larvae. Moreover, bacteria have been found to live symbiotically in the gut of mosquito larvae, where they benefit from the availability of nutrients and a suitable growth medium (Guegan et al. 2018).

The role of bacteria and their volatiles in mediating the oviposition responses of a gravid mosquito is well documented in a number of studies (Poonam et al. 2002, Trexler et al. 2003, Lindh et al. 2008, Ponnusamy et al. 2008, Ponnusamy et al. 2010). Bacterial species producing infochemicals that mediate oviposition behavior in *An. gambiae* have been identified and belong to the genera *Aeromonas, Pasteurella, Pseudomonas, Vibrio,* and *Acetinobacter* (Sumba et al. 2004). Other species such as *Psychrobacter immobilis*, *Sphingobacterium multivorum,* and *Bacillus* species have been shown to significantly stimulate oviposition behavior in *Ae. albopictus* (Trexler et al. 2003).

Infochemicals of bacterial origin have also been shown to mediate oviposition in *Cx. quinquefasciatus* (Beehler et al. 1994), *An. gambiae* (Lindh et al. 2008), and *Ae. aegypti* (Melo et al. 2020) mosquitoes. Culture filtrates of *Bacillus thuringiensis* var. *israelensis* (wild type) and *B. cereus* are known to attract gravid *Cx. quinquefasciatus* better than *p*-cresol (Poonam et al. 2002). Moreover, several species of mosquitoes feed on bacteria during their larval stages (Merritt et al. 1992). Also, cyanobacteria have been associated with high anopheline larval productivity in breeding sites, and the most frequently isolated taxa include: *Phormidium* sp., *Oscillatoria* sp., *Aphanocapsa* cf *littoralis*, *Lyngbya lutea*, *P. animalis*, and *Anabaena* cf. *spiroides* (Vazquez-Martinez et al. 2002, Melo et al. 2020). Recently, it was found that the cyanobacteria *Kamptonema* sp. is attractive to egg-laying *Ae. aegypti*. This attraction was caused by geosmin, a compound produced by *Kamptonema* sp. It is clear that larval mosquito habitats produce infochemicals of microbial origin that mediate mosquito oviposition behavior (Lindh et al. 2015). However, the chemical composition and mode of action of chemicals involved are not yet fully explored.

Bacteria are also involved in the decomposition of organic matter, which leads to emission of volatile compounds that attract gravid mosquitoes to oviposit. In most cases, volatile chemicals produced by decomposition of organic debris are the principal attractants of culicine mosquitoes (Bentley and Day 1989, Mboera et al. 1999, Takken and Knols 1999). Log ponds are particularly attractive oviposition sites for *Cx. tarsalis* and *Cx. quinquefasciatus,* and water contaminated with chicken manure or rice straw infusions are very attractive to *Cx. pallens* (Service 1993). Cow manure infusions attract *Cx. quinquefasciatus* and *Cx. nigripalpus* (Allan et al. 2005), as well as *Cx. pipiens* and *Cx. restuans* (Jackson et al. 2005). Furthermore, it was reported that water polluted by various materials, including rabbit feces, have an additive effect when used with an oviposition pheromone (Agelopoulos et al. 1999). Gas chromatography-mass spectrometry (GC-MS) analysis of the volatiles emitted from these materials identified compounds including phenol and indole. Moreover, the identification of olfactory receptor for 3-methylindole enabled laboratory and field assays using the pure compound, which significantly increased oviposition activity (Mboera et al. 2000b, Hughes et al. 2010).

Pheromones

Pheromones are infochemicals that mediate interactions between individuals of the same species in which the benefit is to the origin-related individual, to the receiver, or to both (Dicke and Sabelis 1988). They can originate from specialized secretory glands, body orifices, and organs involved in digestion and reproduction (e.g., mouth, anus, aedeagus) (Wertheim et al. 2005). Pheromones act as chemical releasers of specific factors that trigger fixed action patterns in mosquitoes, such as aggregation for mating and oviposition. Aggregation pheromones on larval-habitat substrates are often released by other females (Judd and Borden 1992, Jiang et al. 2002, Wertheim et al. 2002) or by eggs, larvae, or pupae (Bentley and Day 1989, Leonard and Saini 1993, McCall and Cameron 1995).

In several dipteran species, pheromones released by females are male-derived. Males produce the pheromone and transfer it to females during copulation (Bartelt et al. 1985, Bentley and Day 1989, Schaner et al. 1989). Examples can be found in the house fly, *Musca domestica,* whereby infochemicals synthesized by the ovaries of gravid females attract other gravid females (Jiang et al. 2002), and several *Culex* species in which oviposition-mediating pheromone can be extracted from eggs (Laurence and Pickett 1982, 1985)

In mosquitoes, oviposition pheromones are known to originate from eggs and larvae of conspecifics (Chadee 1993a, Zahiri et al. 1997, Blackwell and Johnson 2000). This hypothesis was first made when *Cx. tarsalis* was found to have an oviposition preference for water containing conspecific larvae above distilled water (Osgood 1971). The responsible pheromone was identified as a mixture of estrolide 1,3-diglycerides (Starratt and Osgood 1973). Methanolysis of the mixture yielded methyl esters of mono- and dihydroxy fatty acids, of which *erythro*-5,6-dihydroxyhexadecanoic acid was the major component among the dihydroxy compounds. A similar mechanism was observed with *Cx. pipiens*, in which the oviposition response was due to droplets present on the apex of the eggs (Bruno and Laurence 1979). The responsible chemical compound was *erythro*-6-acetoxy-5-hexadecanolide, henceforth called mosquito oviposition pheromone (Laurence and Pickett 1982, 1985, Otieno et al. 1988).

Furthermore, several compounds have been extracted from the eggs of *Ae. aegypti* and identified as 6-hexanolactone, methyl dodecanoate, dodecanoic acid, methyl tetradecanoate, tetradecanoic acid, methyl (Z)-9-hexadecenoate, octadecanoic acid, methyl hexadecanoate (Z)-9-hexadecenoic acid, hexadecanoic acid, methyl (Z)-9-octadecenoate, and methyl octadecanoate (Z)-9-octadecenoic acid (Table 4). All identified chemical compounds deterred gravid *Ae. aegypti*, except dodecanoic and (Z)-9-hexadecenoic acid which showed significant positive oviposition response at different concentrations (Ganesan et al. 2006).

Table 4a. Effects of oviposition cues from living organisms on the response of gravid mosquitoes.

Source of oviposition cue	Species/type emitting	Chemical composition of emitted cues	Effects of the infochemicals	References
Mosquito				
Mosquito eggs	*Cx. quinquefasciatus*	6-acetoxy-5-decanolide	Attracts *Cx. quinquefasciatus*; *Cx. tarsalis and Cx. cinereus*	Laurence & Picket 1982, 1985, Trexler et al. 2003, Braks et al. 2007, Mboera et al. 1999
	Ae. aegypti	Dodecanoic acid (Z)-9-hexadecenoic acid Methyldodecanoate 6-hexanolactone Methylhexadecanoate Hexadecanoic acid Methyl(Z)-9-octadecanoate Methyloctadecanoate Octadecanoic acid (Z)-9-octadecanoic acid Methyltetradecanoate Tetradecanoic acid Methyl(Z)-9-hexadecenoate	*Ae. aegypti* and *Cx. quinquefasciatus* are attracted by dodecanoic and (Z)-9-hexadecenoic acid but deterred by the rest of the chemicals	Ganesan et al. 2006, Sivakumar et al. 2011
Mosquito larvae	*Ae. aegypti*	Heneicosane Octadene Isopropyl myristrate Docosane Nonacosane	Heneicosane was the most attractant to *Ae. aegypti*	Mendki et al. 2000
	An. gambiae	Nonane	Attracts *An. gambiae* and *Cx. quinquefasciatus*	Schoelitzs et al. 2020
		2,4 Pentanedione,	Attracts *An. gambiae*	Schoelitzs et al. 2020
		Dimethyldisulphate, Dimethyltrisulphate	Deters *An. gambiae*	Schoelitzs et al. 2020

Evidence for pheromones of larval origin has been based on chemical analysis of water from larval sites following the observation that certain mosquito species prefer to lay eggs on water containing conspecific larvae but not eggs. This hypothesis was supported by the fact that preference for water that contained conspecific larvae of *Cx. annulirostris* was density dependent (Dhileepan 1997). In a similar way, water from *Ae. aegypti* breeding sites was analyzed and the following compounds were identified: docosane, heneicosane, isopropyl myristate, and nonacosane (Table 4a-d). Heneicosane had the strongest effect on ovipositing *Ae. aegypti* (Mendki et al. 2000). Recently, two larval oviposition pheromones of *An. gambiae* were reported: nonane and 2,4-pentanedione (2,4-PD) were identified in the headspace of larvae of *An. coluzzii*. The compounds were shown to attract gravid females of *An. coluzzii* and *An. gambiae s.s.* Interestingly, in the same study, it was found that in association with late stage larvae, the sulfides dimethyldisulfide (DMDS) and diethyltrisulfide (DMTS) were produced, DMDS and DMTS suppressed the attractive effect of the pheromones and caused a high degree of egg retention (Schoelitsz et al. 2020). The production of the larval pheromones was not stage dependent, while that of DMDS and DMTS appeared only at a late stage in larval development. The net effect of these interactions was that young larvae stimulate females to oviposit in their site, while older larvae detered females from doing so.

MOSQUITO RESPONSES TO OVIPOSITION INFOCHEMICALS

Site location and selection

Before and during oviposition, many mosquito species exhibit several behavioral and physiological traits. Although for most species, pheromones have yet to be fully characterized, efforts to identify their roles have implicated long-range attractive and short-range arresting constituents. For example, in several laboratory studies, it was suggested that at long range, acetoxyhexadecanolide stimulates upwind flight of *Cx. quinquefasciatus* towards the pheromone source and at close range, this compound produces an orthokinetic reduction in flight speed (Pile et al. 1991, 1993). Moreover, at an oviposition site, the pheromone induces a higher proportion of visiting females to oviposit. This suggests that the same infochemical can elicit different behavioral responses when the gravid mosquito is near or far from a prospective breeding site. However, the role that the infochemical plays

Table 4b. Effects of oviposition cues from living organisms on the response of gravid mosquitoes.

Source of oviposition cue	Species/type emitting	Chemical composition of emitted cues	Effects of the infochemicals	References
Fungi	*Fusarium falciforme*	Cedrol	Attracts *An. arabienis, An. gambiae*	Eneh et al. 2016a
	Polyporous spp	Unknown	Attracts *An. subpictus* Attracts *Ae. aegypti* Deters *Cx. quinquefasciatus*	Sivagnaname et al. 2001
	Tricoderma viride	Unknown	Attracts *Cx. quinquefasciatus*	Geetha et al. 2003
Protist	*Ascogregarina taiwanensis*	Unknown	Attracts *Ae. aegypti*	Reeves 2004
Yeast	*Candida* near *pseudoglaebosa*	Unknown	Attracts *Ae. aegypti*	Reeves 2004
Trematode	*Plagiorchis elegans*	Unknown	Deters *Ae. atropalpus*	Zahiri et al. 1997
Predators				
Dragonfly	*Anax imperator*	Unknown	Deters *C. longiareolata*	Stav et al. 1999
Diving beetle	*Eretes griseus*	Unknown	Deters *Cx. tritaeniorhynchus*	Ohba et al. 2012
Backswimmer	*Notonecta maculata*	Unknown	Deters *C. longiareolata* and *An. gambiae*	Spencer et al. 2002, Blaustein et al, 2004, Munga et al. 2006, Silberbush et al. 2011
Tadpole	*Limnodynastes peronei*	Unknown	Deters *O. australis*	Mokany & Shine 2003
	Bufo viridis	Unknown	Deters *C. longiareolata*	Blaustein & Kotler 1993
Copepods	*Mesocyclops longisetus*	3-carene, α-terpinene, α-copaene, α-longipinene, α-cedrene, δ-cadinene	Attracts *Ae. aegypti*	Torres-Estrada et al. 2001
Molluscs:				
Carpet shell	*Paphia undulata*	Unknown	Attracts *Ae. albopictus*	Thavara et al. 2004
Giant tiger prawn	*Penaeus monodon*			
Fishes	*Gambusia affinis*	Unknown	Deters *Cx. pipiens* & *Cx. quinquefasciatus*	Angelon et al. 2002
			Deters *Cx. tarsalis*	Van Dam & Walton 2008
	Betta splendens	Unknown	Deters *Ae. aegypti*	Cavalcanti et al. 2009, Pamplona et al. 2009

in space, and the distance over which infochemicals are effective, requires similar investigations with other species of mosquitoes.

Additive and synergistic effects

The oviposition response of mosquitoes to a mixture of attractants has been of great interest recently. In a natural setting, various cues are available to gravid mosquitoes and therefore what has been observed is likely to be a response to multiple stimuli. Most likely there are interactions between pheromones and other infochemicals in guiding gravid mosquitoes to suitable oviposition sites (McCall and Cameron 1995). For example, when the synthetic oviposition pheromone (SOP) (6-acetoxy-5-hexadecanolide) was mixed with grass infusion, or soakage pit water, more egg rafts of *Cx. quinquefasciatus* were laid in the mixture compared to the response of individual attractants alone (Mboera et al. 1999). This means that SOP has a synergistic effect with grass infusion or soakage pit water in attracting female *Cx. quinquefasciatus*.

The response of *Cx. quinquefasciatus* to blends of a fixed amount of SOP with variable doses of 3-methylindole has additive rather than synergistic effects (Millar et al. 1994). The oviposition response of *Cx quinquefasciatus* to the blend increased gradually to a threshold of 0.1 mg. At higher doses, oviposition deterrence was observed. When tested separately at the same dose, which as a blend was repellent, the infochemicals attracted mosquitoes. Additive effects of SOP and 3-methylindole have been observed with *Cx. quinquefasciatus* in different geographical areas (Mboera et al. 2000b, Olagbemiro et al. 2004). Several products originating from soil microbes (Herrera-Varela et al. 2014), plant microbes, and conspecific larvae (Mwingira et al. 2019) have been shown to attract ovipositing gravid anopheline mosquitoes. Of particular interest is cedrol, which originates from fungi living in rhizomes of the grass *Cyperus rotundus* and attracts both *An. gambiae* and *An. arabiensis* (Eneh et al. 2016a). As oviposition in nature is mediated by several cues, such individual compounds can be combined to realize their additive or synergistic effects.

Activation of odorant receptors

The *An. gambiae* protein AgOr1, a female-specific member of a family of putative odorant receptors (Fox et al.

Table 4c. Effects of oviposition cues from living organisms on the response of gravid mosquitoes.

Source of oviposition cue	Species/type emitting	Chemical composition of emitted cues	Effects of the infochemicals	References
Microorganisms				
Bacteria	*Pseudomonas aeruginosa*	7,11-dimethyl-octadecane	Attracts *Ae. aegypti*	Ikeshoji et al. 1979
	Psychrobacter immobilis	Unknown	Attracts *Ae. albopictus*	Trexler et al. 2003
	Sphingobacterium multivorum			
	Bacillus spp			
	Pseudomonas	Chemical compounds produced by these bacteria are not known	Except for *S. matrophilia* that deterred *An. gambiae,* odor from all other bacteria attracted *An. gambiae*	Huang et al. 2006
	Stenotrophomonas			
	Enterobacter			
	Pantoea,			
	Klebsiella,			
	Acinetobacter			
	Aeromonas			
	Bacillus			
	S. matrophilia			
	Vibrio metchnikovii	2-Methyl-3-decanol	Attracted *An. gambiae*	Lindh et al. 2008
	Proteus spp	3-Methyl-1-butanol, Indole, 2-phenyl ethanol		
		3-Methyl-1-butanol		
	Micrococcus spp	3-Methyl-1-butanol, 3-Methylbutanoic acid		
	Exiguobacterium spp	Alkyl-pyrazines		
		Phenylmethanol		
	Bacillus spp	2-phenylethanol		
	Comamonas spp			
	Unknown species	Carboxylic acid and Methyl esters	Attracts *Ae. aegypti*	Ponnusamy et al. 2008, 2010
	Aeromonas	Unknown	Deters *An. sinensis*	Li Mei and Tang Lin-Hua 2010
	Cyanobacteria (*Kamptonema* sp.)	Geosmin	Attracts *Ae. aegypti*	Melo et al. 2020
	Leptolyngbya	Unknown	Volatiles from cynobacterial mats attract *An. albimanus* and *An. vestitipennis* when at low concentrations.	Rejmankova et al. 2005

2001, Hill et al. 2002), has been found to respond to certain chemicals found in mosquito larval habitats (Xia et al. 2008). This suggests that chemical oviposition cues activate receptors of this type and may attract the mosquito to suitable sites. Most of the sensory physiology studies undertaken to explore olfactory receptor neural responses in mosquitoes suggest that various infochemicals induce physiological responses (Costantini et al. 2001). Single sensillum electrophysiology (SSR) has revealed that 4-methylphenol, a known oviposition infochemical, confers a strong response in the AgOr1 protein (Hallem et al. 2004). Consequently, chemical cues that were shown to mediate oviposition can be used to identify neurons responsible for the observed attraction to oviposition sites and determine the sensitivity of identified neurons to other putative behavioral compounds. Increasingly, interactions between behavioral and sensory physiology studies are used for the rapid identification of relevant infochemicals (Zwiebel and Takken 2004, Ray 2015, Lombardo et al. 2017). Thus, knowledge of changes in olfactory sensitivity to kairomones can be applied to increase trap catches of malaria mosquitoes that have taken a blood meal and need to locate an oviposition site (Qiu et al. 2013).

Group oviposition

In dipterans, pheromones are often used in the context of aggregated oviposition within species (Bentley and Day 1989, Jiang et al. 2002). Although the benefits of group oviposition in mosquitoes have not been studied in detail, in most insects aggregation is suggested to help conspecifics to find a food source. However, for an aggregation trait to evolve, both the gravid mosquito and the immature or their associated microbes must benefit to some degree. Generally, the benefits of pheromone-induced aggregation in insects have been categorized as increasing the efficiency of resource

Table 4d. Effects of oviposition cues from living organisms on the response of gravid mosquitoes.

Source of oviposition cue	Species/type emitting	Chemical composition of emitted cues	Effects of the infochemicals	References
Plants				
Bamboo grass	*Arundinaria gigantea*	Unknown	Attracts *Cx. stigmatosoma*	Beehler et al. 1994
Bermuda grass	*Cynodon dactylon*	3-methylindole, 4-methylphenol, 4-ethylphenol	Attracts *Cx. tarsalis* and *Cx. quinquefasciatus* The phenols were neither attractive nor deterrent	Beehler et al. 1994, Mboera et al. 2000b, Millar et al. 1992, Blackwell et al. 1993
Other grasses	*Brachiaria mutica, Jouvea staminea, Fimbristylis spadicea ,Ceratophyllum-demersum*	Guaiacol Phenol Isoeugenol Longifolene Caryophyllene Phenyl ethyl alcohol P-cresol	Higher concentrations deterred while lower concentrations attracted *An. albimanus*	Torres-Estrada et al. 2005
Cattails	*Typha domingensis*	Unknown	Volatiles from *Typha domingensis* and cyanobacterial mats attract *An. albimanus* and *An. vestitipennis* when at low concentrations. At higher concentrations egg laying is reduced	Rejmankova et al. 2005
	Typha latifolia	Unknown	Attracts *Coquillettidia pertubans*	Serandour et al. 2010
Algae	*Spyrogyra majuscule;, Cladophora glomerata*	Unknown	Attracts *An. pseudopuctipennis*	Bond et al. 2005, Rejmankova et al. 2005
White oak	*Quercus alba*	Unknown	*Ae. aegypti was* attracted to infusions made over short time fermentation period while *Ae. albopictus* was attracted to infusions made over long fermentation period.	Ponnusamy et al. 2012
Leaves			*Ae. triseriatus* deposited largest number of eggs in older age infusion	Trexler et al. 1998
Hard orange	*Poncirus trifoliata*	Poncirin, Rhoifolin, Naringin, Marmesin	The flavonoids exhibited oviposition deterrence against *Ae. aegypti*, and are ovicidal at higher concentrations	Rajkumar and Jebanesan 2008
Water oak	*Quercus nigra*	Unknown	Attracts *Ae. albopictus*	Obenauer et al. 2012
Longleaf pine	*Pinus palustris*	Unknown	Deters *Ae. albopictus*	
Industrial fertilizers	NPK	Aqueous solution of Nitrogen, Phosphorus and Potassium	Moderate concentration of aqueous solution attracted *Ae. aegypti.* Low or high concentrations did not induce significant attraction	Darriet and Corbel 2008, Darriet et al. 2010

use, finding mates, protection from natural enemies, and protection from environmental conditions (Wertheim et al. 2005). Also, pheromone-induced aggregation results in competition among and between species inhabiting the same niche. Such competition may favor one species over the other and alter the distribution or abundance of competing species (Shragai et al. 2019).

Moreover, the increase in numbers of eggs and larvae may provide physical protection of the group or increased availability of food source in case the emitter of the cue is a microbe. For *Culex* species, a large number of larvae may prevent the formation of scum on top of an organically rich oviposition site (McCall and Cameron 1995). Thus, by forming groups, mosquitoes may change the existing environment to their advantage. Aggregation behavior ensures high egg density at the oviposition site and resultant spatial cohesiveness of the progeny, which means communal aggregation. As a result, oviposition in mosquitoes constitutes a principal means of transmitting genetic traits to the progeny and facilitating accumulation of these traits across generations (Wong et al. 2012)

Attracting natural enemies

Aggregated oviposition means an increase in the number of mosquito larvae in a limited area, which often results in resource competition among larvae. Mosquito larval competition can have large effects on emerging adults in terms of longevity, adult size, and mating success (Agudelo-Silva and Spielman 1984). Studies with *Cx. pipiens* suggest that larval resource availability and competition influence mosquito population growth correlates and have lasting effects on traits that relate to a mosquito's ability to vector pathogens (Alto et al. 2012). Studies of *An. gambiae* indicate that competition within the larval environment may indirectly regulate their population by reducing adult body size, which in turn reduces adult survivorship and fecundity (Gimnig et al. 2001, Takken et al. 2013).

On the other hand, aggregation pheromones may also enhance the chances that the site is located by competitors and/or natural enemies (Wertheim et al. 2005). Competitors and predators are able to use the same infochemicals as mosquitoes use to their benefit. In this way, a mosquito pheromone is a kairomone for competitors and natural enemies. For example, the compound (5R, 6S)-6-acetoxy-5-hexadecanolide, which is the oviposition pheromone of *Cx. quinquefasciatus,* also attracts *Cx. tarsalis, Cx. cinereus,* and *Cx. tigripes* to lay eggs at the same oviposition sites (Mboera et al. 1999). The latter three species are potential competitors of *Cx. quinquefasciatus* and interestingly, *Cx. tigripes* larvae are efficient predators of *Cx. quinquefasciatus* larvae (Mboera 1999).

Apart from these observations, overcrowding and resource competition reduces overall adult fitness (Yoshioka et al. 2012). This may render the resulting mosquito population susceptible to infection by pathogenic microbes (Alto et al. 2008). Despite the risks of aggregation behavior to safety and individual fitness, mosquitoes continue to respond to aggregation pheromone that indicates the presence of a safe site. The majority of mosquito species suffer serious mortality due to the presence of predators in breeding sites and have developed a chemical sense to detect and avoid these enemies (Table 1). Gravid mosquitoes of several species can detect predators in prospective breeding sites and divert egg laying activity. These include *Culex* mosquitoes (Blaustein et al. 2005), *C. longiareolata,* and *An. gambiae* (Munga et al. 2006, Warburg et al. 2011). Therefore, in theory, the benefits of laying eggs in a safe site outweigh the costs of larval competition.

Multiple functions

Infochemicals that mediate mosquito oviposition behavior have multiple functions depending on their emission rate. In most cases, mosquitoes are attracted to a chemical when presented at low concentration and deterred at high concentration (Hoffmann and Miller 2002). When the emission of chemicals from the source is low, mosquitoes are stimulated to lay eggs, while when the emission is high, they are deterred. For example, in *An. gambiae,* oviposition is stimulated by low larval density and inhibited by high larval density (Sumba et al. 2008). Similarly, *An. albimanus* and *An. pestitipennis* are attracted to low concentrations of organic extracts, while deterred from high concentrations of organic extracts (Rejmankova et al. 2005, Torres-Estrada et al. 2005).

POTENTIAL APPLICATION OF OVIPOSITION INFOCHEMICALS

Infochemicals affect insect behavior in nature. Humans exploit this knowledge by introducing artificial chemicals for behavioral manipulation. Infochemicals that mediate oviposition in mosquitoes may play an important role in disease and vector control strategies in the future. Some of these potential applications are discussed below.

Vector surveillance

Mosquito sampling is a prerequisite to most vector population studies (Githeko et al. 1994, WHO 2017), and therefore various sampling techniques as well as entomological indicators have been used to monitor and evaluate the impact of vector control interventions (Mboera 2005). Ovitraps are often used for mosquito population monitoring and surveillance (McHugh and Hanny 1990). These traps can also be used to estimate vector population size and structure. The use of oviposition attractants or stimulants as baits, to increase the sensitivity of these traps as well as gravid female traps, has considerable potential (Freier and Francy 1991). Such traps have been effectively used to sample gravid mosquitoes (Mboera et al. 2000a) or attract them to breeding sites treated with a biocide (Mboera et al. 2003, Kampen et al. 2015, Suter et al. 2016).

Most *Anopheles* mosquitoes tend to rest in a sheltered place after a blood meal, and they remain resting until eggs are fully developed, after which they fly out in search of a suitable oviposition site (Klowden and Blackmer 1987, Takken et al. 2001). However, some do not rest in human-made shelters; they fly out and rest in natural shelters. Sampling gravid females by using oviposition attractants could be very rewarding, as gravid females will be attracted from various resting places, even those of species that are not sensitive to other methods of trapping. Therefore, traps baited with an oviposition pheromone are likely to be more efficient and thus are excellent tools for detecting the presence of mosquitoes, monitoring their flight range as well population levels.

Gravid female traps have been used not only for the surveillance of vector populations, but also for the surveillance of vector-borne diseases (Allan and Kline 2004). The entomological parameter being studied and the behavior of the mosquito species being sampled determine the choice of a sampling method (Davis et al. 1995). Unfortunately, most of the available mosquito sampling methods may not allow for such rational choices to be made, as there are major limitations associated with their use (Service 1977). Consequently, new tools for sampling mosquito populations are required to determine various entomological parameters of epidemiological importance.

Oviposition pheromones that specifically attract gravid mosquitoes exposed to infection during their previous blood meals can be used in traps to aid the determination of population infection rates more effectively than traps that attract host-seeking mosquitoes (McCall and Cameron 1995). Traps baited with chemical oviposition stimuli can aid effectively in the estimation of the entomological inoculation rate (EIR), which is the standard parameter for estimating transmission, representing the number of infectious bites any person receives per year (Smith et al. 2006, Kilama et al. 2014). As the likelihood of getting sick is influenced by EIR, its estimation is important for disease monitoring. It follows that the use of infochemicals affecting oviposition in vector surveillance can increase the chance of sampling mosquitoes that are infected with parasites. Therefore, when released from mosquito traps, oviposition infochemicals will provide an objective monitoring tool for parasite transmission.

Control of adult mosquitoes

In addition to increasing the sensitivity for monitoring population and surveillance, the use of oviposition infochemicals in traps has a potential role in the control of adult gravid mosquitoes when traps are inoculated with a suitable pesticide (Mboera et al. 2003). Lethal ovitraps with an oviposition strip treated with deltamethrin insecticide have been found to affect natural populations of *Ae. aegypti* (Perich et al. 2003, Sithiprasasna et al. 2003). Traps baited with a synthetic oviposition pheromone, authentic plant volatiles, or a blend of these chemicals are expected to become excellent tools for the control of gravid mosquitoes particularly when combined with an environmentally-friendly pesticide such as insect growth regulators (IGRs). Some IGRs, such as pyriproxyfen (Chism and Apperson 2003, Mbare et al. 2019) and methoprene (Nishiura et al. 2003, Braga et al. 2005b, Braga et al. 2005a), are highly active against mosquitoes; consequently, when used in combination with oviposition infochemicals, they may provide a novel approach to mosquito control. When combined with insect-growth regulators in Kenya, the pheromone directed egg-laying and inhibited adult emergence of *Culex* (Otieno et al. 1988). This is a highly selective method of vector control with the advantage that it immediately reduces the density of targeted species with relatively little or no harm to the environment. In other insect species, however, infochemicals are already widely used for population regulation (Gitau et al. 2013, Kelly et al. 2014).

Control of the immature stages

Oviposition infochemicals have considerable potential for delivery of pathogens or pesticides to larval populations (Otieno et al. 1988, Schlein and Pener 1990, Itoh et al. 1994). It has been demonstrated with *Cx. quinquefasciatus* that oviposition attractants might be employed to lure mosquitoes to sites already treated with ovicidal compounds (Barbosa et al. 2010). With more knowledge of mosquito oviposition behavior, source-reduction programs can more effectively focus on the most productive breeding sites, which resulted from pheromone-induced group oviposition behavior (Kaur et al. 2003). Consequently, larval control through environmental management or by using biolarvicides will become efficient and cost-effective when the targeted habitats are clustered or when the target area size is limited (Utzinger et al. 2001, Killeen et al. 2002, Fillinger et al. 2003). Attempts to lure gravid mosquitoes to sites already treated with pesticides have been made in Brazil (Barbosa and Regis 2011), Malaysia (Ong and Jaal 2015), Tanzania (Schorkopf et al. 2016), Peru, and Thailand (Paz-Soldan et al. 2016).

Relatively few studies using the natural biocides *Bacillus thuringiensis israelensis/B. sphaericus* have been carried out against African malaria vectors (Seyoum and Abate 1997, Skovmand and Sanogo 1999, Fillinger et al. 2003) and they were restricted to experimental and operational research (Barbazan et al. 1998, Dambach et al. 2019, Fillinger et al. 2009, Imbahale et al. 2012, Mazigo et al. 2019, Mpofu et al 2016). Studies conducted in Tanzania and Kenya indicated that biolarviciding is a cost-effective intervention even in rural settings (Rahman et al. 2016, Derua et al. 2019b). The efficacy of *B. thuringiensis israelensis (Bti)* use for malaria control was for the first time reviewed in a major study comparing all studies known to-date (Choi et al. 2019). Recent studies have underlined the potential of larval control using microbial insecticides and deserve broader application and dissemination (Derua et al. 2019a).

The use of biolarvicides has a great advantage over all other larvicides, as they have a low probability of causing environmental pollution or developing resistance (Charles and Nielsen-LeRoux 2000). Focusing research on the integration of pesticides with oviposition infochemicals will provide the basis for successful use of infochemicals for vector control as an alternative to exclusive use of broad-spectrum pesticides. Consequently, there is a great potential of using oviposition infochemicals to manipulate Afro-tropical malaria vectors by leading them to traps or sites treated with biolarvicides.

Disease prevention

Knowledge of mosquito dispersal is critical for vector-borne disease control and prevention strategies and for understanding population structure and pathogen dissemination (Harrington et al. 2005). An increase in adult mosquito dispersal could be a result of gravid females searching for suitable breeding sites, and so a shortage of suitable oviposition sites may accelerate the dispersal of adult females. Larval habitat reduction may encourage the dispersal of these vectors in their search for oviposition sites and thereby contribute to the spread of diseases (Edman et al. 1998). Dispersal is influenced by prevailing wind, longevity of the species, and by the presence of a suitable breeding site. The suitability of a breeding site is generally assessed by gravid mosquitoes through the presence of chemical oviposition cues. Therefore, the deployment of oviposition attractants in artificial oviposition sites would restrict gravid female mosquitoes from dispersing in search of oviposition sites and enhance the efficacy of mosquito control for the prevention of vector-borne disease (Mafra-Neto and Dekker 2019).

CONCLUSIONS AND FUTURE PROSPECTS

Ecological conditions under which infochemicals mediate oviposition behavior are similar among a wide range of mosquito species from different taxonomic tribes. This enables us to draw general conclusions on the possibility of exploiting mosquito oviposition behavior and propose a novel strategy for mosquito surveillance and control. Although some of the earliest studies of the role of infochemicals in the biology of mosquitoes were promising, exploitation of knowledge on chemical ecology for the development of potential control strategies has received limited attention. Further elucidation of the role of infochemicals in mosquito oviposition may lead to a viable and effective tool for vector control. Studies on culicine mosquitoes have demonstrated that we have only just started to unravel the rich and complex chemical communication systems of these important insects.

In this review we have summarized the roles that infochemicals play in the behavioral pattern and responses of the oviposition phase of mosquitoes. In the last decade much progress has been made in the discovery of infochemicals mediating oviposition behavior of anophelines. We conclude that there is a great potential of utilizing infochemicals mediating oviposition behavior in mosquitoes for the development of vector surveillance and control strategies. Studies on culicine mosquitoes and the recent findings obtained from research on anopheline spp. provide a useful model for more studies on these and other mosquito genera.

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