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Chemosensory Cues for Mosquito Oviposition Site Selection

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ABSTRACT Gravid mosquitoes use chemosensory (olfactory, gustatory, or both) cues to select oviposition sites suitable for their offspring. In nature, these cues originate from plant infusions, microbes, mosquito immature stages, and predators. While attractants and stimulants are cues that could show the availability of food (plant infusions and microbes) and suitable conditions (the presence of conspecifics), repellents and deterrents show the risk of predation, infection with pathogens, or strong competition. Many studies have addressed the question of which substances can act as positive or negative cues in different mosquito species, with sometimes apparently contradicting results. These studies often differ in species, substance concentration, and other experimental details, making it difficult to compare the results. In this review, we compiled the available information for a wide range of species and substances, with particular attention to cues originating from larval food, immature stages, predators, and to synthetic compounds. We note that the effect of many substances differs between species, and that many substances have been tested in few species only, revealing that the information is scattered across species, substances, and experimental conditions.

KEY WORDS mosquito, odor, olfactory, gustatory, oviposition

Introduction

Mosquito aquatic stages are restricted in their movement and are not able to change their habitats at the larval and pupal stage. Therefore, gravid females should carefully choose oviposition sites. The availability of food, absence of predators, and low levels of competition are among the likely factors sought for.

Olfactory cues range relatively long distances and could convey information for the oviposition seeking gravid females about the substrate's suitability. Therefore, mosquitoes depend mainly on olfactory cues such as the smell of nutrients, cues from predators or other mosquito larvae in the water to decide whether this water is suitable for their larvae or not. For short range substrate evaluation, mosquitoes might use a combination of gustatory, tactile, and even visual cues (Bentley and Day 1989). Here, we focus on the chemosensory component.

An "oviposition attractant" is a substance that causes gravid females to make oriented flight toward the oviposition substrate while an "oviposition stimulant" is a substance that elicits the oviposition behavior after landing on the substrate. On the other hand, a "repellent" is a substance that encourages mosquito to make oriented flight away from the oviposition substrate while a "deterrent" is a substance that inhibits oviposition behavior (Clements 1999). Hence, attractants and repellents are cues that affect mosquito behavior over a long distance and are exclusively olfactory, while stimulants and deterrents act at short range and may include both olfactory and gustatory modalities.

To test a stimulant or deterrent effect of a specific cue, oviposition cages can be used in which mosquitoes are given a choice of different oviposition substrates, and the effect of each substrate on oviposition is assessed based on the number of eggs it receives (Millar et al. 1992, Allan and Kline 1995). On the other hand, olfactometers can be used to identify attractants and repellents (Seenivasagan et al. 2009, 2010). Many different olfactometer designs have been used in different research projects (e.g. one chamber, Y tube, T maze olfactometers). In addition, sticky screen cups to which mosquitoes could be attracted and trapped are also used in some studies to test attractants and repellents (Ponnusamy et al. 2010a,b). In semi field experiments (big field cages) or open field studies, ovitraps (oviposition containers) are used to measure how many eggs a certain substance (deterrent or stimulant) receives (Reiter et al. 1991, Allan and Kline 1995) while traps for gravid mosquitoes are used to test mosquito attraction toward an odor (attractant or repellent; McPhatter and Debboun 2009).

Different mosquito species live in a wide range of habitats and exploit different types of food (Merritt et al. 1992). Consequently, a suitable oviposition substrate for one species could be unsuitable for another. While some oviposition cues are effective across mosquito species, others are species specific. Some attractant or stimulant in one species may be a repellent or deterrent in another species. Furthermore, larval experience could also play a role in altering the otherwise

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Table 1. Cues of plant origin and their effect on the oviposition of different mosquito species

Cue Infusions	Attractant	Repellent	Stimulant	Deterrent
White oak (*Quercus alba*)	*Ae. albopictus*[1,2] *Ae. aegypti* [1,2]	*Ae. aegypti*[1,2]	*Ae. albopictus*[3] *Ae. triseriatus*[3] *Ae. aegypti*[4]	*Ae. triseriatus*[3]
Live oak (*Quercus virginiana*)	*Cx. quin.*[5] *Cx. nigripalpus*[5] *Cx. erraticus*[5]			
Bermuda grass/hay (*Cynodon dactylon*)	*Ae. albopictus*[2,6] *Cx. quin.*[5,7] *Cx. nigripalpus*[5] *Cx. erraticus*[5] *Cx. tarsalis*[7,8]	*Ae. aegypti*[2]	*Ae. aegypti*[9] *Cx. quin.*[7,10] *Cx. tarsalis*[7,8] *Ae. albopictus*[6]	*Ae. aegypti*[6] *Ae. albopictus*[6]
Acacia (*Acacia schaffneri*)	*Cx. quin.*[5] *Cx. nigripalpus*[5] *Cx. erraticus*[5]			
Water oak (*Quercus nigra*)	*Ae. albopictus*[11]		*Ae. albopictus*[11]	
Longleaf pine (*Pinus palustris*)		*Ae. albopictus*[11]	*Ae. albopictus*[11]	
St. Augustine grass (*Stenotaphrum secundatum*)	*Ae. albopictus*[11]		*Ae. albopictus*[11]	
Bamboo (*Arundinaria gigantea*)	*Ae. albopictus*[1,2] *Ae. aegypti*[1,2]		*Ae. aegypti*[4]	
Bamboo (*Bambusa* spp.)			*Ae. aegypt*[12]	
Hackberry leaf (*Celtis occidentalis*)	*Ae. albopictus*[2] *Ae. aegypti*[2]			
Digitaria sp. grass	*Cx. quin.*[13]		*Cx. quin.*[14] *Cx. cinereus*[14] *Cx. tigripes*[14]	
Eleusine indica grass			*Cx. quin.*[15,16]	
Panicum maximum	*Ae. aegypti*[17]		*Ae. aegypti*[17,18] *Ae. albopictus*[18] *Ae. spp.*[18]	
Alfalfa hay	*Cx. quin.*[19]		*Ae. aegypti*[19] *Cx. quin.*[19]	
Cynadon plectosa			*Ae. aegypti*[18] *Ae. albopictus*[18]	
Pennisetum purpureum			*Ae. aegypti*[18]	
Plant extracts				
Ageratum houstonianum leaves				*Ae. aegypti*[20] *Cx. quin.*[20] *A. stephensi*[20]
Artemisia annua				*Ae. aegypti*[21] *Cx. quin.*[21] *A. sinensis*[21]
Cynodon dactylon, *Jouvea straminea*, *Fimbristylis spadicea*, *Ceratophyllum demersum*, *Brachiaria mutica*			*A. albimanus*[22]	*A. albimanus*[22]
Water soluble lectin of *Moringa oleifera*			*Ae. aegypti*[23,17]	
Solenostemma argel				*Cx. pipiens*[24]
Cassia obtusifolia				*A. stephensi*[25]
Aegle marmelos, *Andrographis lineata*, *Cocculus hirsutus*				*A. subpictus*[26]
Solanum trilobatum leaves				*A. stephensi*[27]
Eugenia jambolana, *Solidago canadensis*, *Euodia ridleyi*, *Spilanthes mauritiana* leaves				*Ae. aegypti*[28] *Cx. quin.*[28] *A. stephensi*[28]
Andrographis paniculata				*A. stephensi*[29]
Plant oils				
Rosemary (*Rosemarinus officinalis*)				*Ae. aegypti*[30 31]
Peppermint (*Mentha piperita*)				*Ae. aegypti*[31]
Basil (*Ocimum basilicum*)				*Ae. aegypti*[31]
Citronella (*Cymbopogon nardus*)				*Ae. aegypti*[31]
Celery seed (*Apium graveolens*)				*Ae. aegypti*[31]
Compounds isolated from plants or their infusion				
4-Methylphenol (*p*-cresol)	*Cx. quin.*[7] *Cx. tarsalis*[7] *Ae. triseriatus*[32,33] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	*Ae. albopictus*[35] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	*Ae. aegypti*[36,37] *Ae. albopictus*[6] *Cx. quin.*[38,39] *Cx. tarsalis*[7] *Ae. triseriatus*[32,33] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	*Ae. aegypti*[6,37] *Tx. moctezuma*[34] *Tx. amboinensis*[34]
2-Methylphenol (*o*-cresol)	*Tx. moctezuma*[34] *Tx. amboinensis*[34]		*Ae. triseriatus*[33] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	
3-Methylphenol (*m*-cresol)	*Tx. moctezuma*[34] *Tx. amboinensis*[34]		*Ae. triseriatus*[33] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	*Ae. aegypti*[37]

(*Continued*)

Table 1. (continued)

Cue Infusions	Attractant	Repellent	Stimulant	Deterrent
2-Tridecanone	*Cx. quin.*[7]			
Indole	*Cx. tarsalis*[7]	*Cx. quin.*[7]	*Cx. quin.*[10] *Cx. tarsalis*[7]	*Ae. albopictus*[6]
Naphthalene			*Cx. tarsalis*[7]	
4-Methylcyclohexanol	*Ae. triseriatus*[33] *Tx. moctezuma*[34] *Tx. amboinensis*[34]		*Ae. triseriatus*[33] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	
3-Methylindole (Skatole)			*Ae. albopictus*[6] *Ae. aegypti*[36]	*Ae. albopictus*[6] *Ae. aegypti*[6]
	Cx. quin.[7,38,40] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	*Cx. quin.*[7] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	*Cx. quin.*[10,16,38,39,41,42] *Cx. tarsalis*[7,38] *Cx. stig.*[38] *Tx. moctezuma*[34] *Tx. amboinensis*[34]	*Cx. quin.*[41,43] *Tx. moctezuma*[34] *Tx. amboinensis*[34]
Trimethylamine	*Cx. quin.*[40]			
Dimethyltrisulfide	*Cx. tarsalis*[7]	*Cx. quin.*[7]		
Phenol	*Cx. tarsalis*[7]		*Ae. aegypti*[6,36]	*Ae. albopictus*[6] *Ae. aegypti*[6]
2,4-Dimethylphenol	*Ae. triseriatus*[33]		*Ae. triseriatus*[33]	
2,3-Dimethylphenol			*Ae. triseriatus*[33]	
4-Ethylphenol			*Ae. aegypti*[6] *Ae. triseriatus*[33]	*Ae. albopictus*[6] *Ae. aegypti*[6]
Camphor			*Ae. aegypti*[30]	
β-Pinene			*Ae. aegypti*[30]	
Borneol			*Ae. aegypti*[30]	
Borneol acetate			*Ae. aegypti*[30]	
Cineol				*Ae. aegypti*[30]
Citronellal				*Ae. aegypti*[30]
Eugenol				*Ae. aegypti*[30]
Linalool				*Ae. aegypti*[30]
p-Cymene				*Ae. aegypti*[30]
Pulegone				*Ae. aegypti*[30]
Trans-anethole				*Ae. aegypti*[30]
Thymol				*Ae. aegypti*[30]
Nonanal	*Cx. quin.*[7,40] *Cx. tarsalis*[7]		*Cx. tarsalis*[7]	
Confertifolin				*Ae. albopictus*[45]

Citations: [1] (Ponnusamy et al. 2010a), [2] (Ponnusamy et al. 2010b), [3] (Trexler et al. 1998), [4] (Ponnusamy et al. 2008), [5] (McPhatter and Debboun 2009), [6] (Allan and Kline 1995), [7] (Du and Millar 1999), [8] (Isoe et al. 1995), [9] (Reiter et al. 1991), [10] (Millar et al. 1992), [11] (Obenauer et al. 2010), [12] (Arbaoui and Chua 2014), [13] (Mboera et al. 2000a), [14] (Mboera et al. 1999), [15] (Barbosa et al. 2007), [16] (Barbosa et al. 2010b), [17] (Santos et al. 2014), [18] (Sant'ana et al. 2006), [19] (Hazard et al. 1967), [20] (Tennyson et al. 2012), [21] (Cheah et al. 2013), [22] (Torres-Estrada et al. 2005), [23] (Santos et al. 2012), [24] (Al-Doghairi et al. 2004), [25] (Rajkumar and Jebanesan 2009), [26] (Elango et al. 2009), [27] (Rajkumar and Jebanesan 2005), [28] (Prathibha et al. 2014), [29] (Chenniappan and Kadarkarai 2008), [30] (Waliwitiya et al. 2009), [31] (Warikoo et al. 2011), [32] (Bentley et al. 1979), [33] (Bentley et al. 1981), [34] (Collins and Blackwell 2002), [35] (Trexler et al. 2003a), [36] (Baak-Baak et al. 2013), [37] (Afify and Galizia 2014), [38](Beehler et al. 1994), [39] (Geetha et al. 2003), [40] (Leal et al. 2008), [41](Blackwell et al. 1993), [42] (Mboera et al. 2000b), [43] (McCall and Eaton 2001), [44] (Olagbemiro et al. 2004), [45] (Maheswaran and Ignacimuthu 2014).

Ae., *Aedes*; *Cx.*, *Culex*; *Cx. quin.*, *Culex quinquefasciatus*; *Cx. stig.*, *Culex stigmatosoma*; *A.*, *Anopheles*; *Tx.*, *Toxorhynchites*.

innate site selection behavior (McCall and Eaton 2001).

In this review, olfactory and gustatory cues that influence oviposition are summarized in Table 1–5 according to their effect (stimulant or attractant, or deterrent or repellent), their source in nature, and the information they provide to oviposition seeking mosquitoes. Some of these cues show concentration dependent variability. For example, 3-methylindole is a repellent at 0.01 µg/liter but an attractant at 1 and 10 µg/liter for *Culex quinquefasciatus* Say (Du and Millar 1999). In other cases, the published data are contradictory. For example, 4-methylphenol (*p*-cresol) has been reported as a stimulant or deterrent for *Aedes aegypti L.* at similar concentrations in different studies (Allan and Kline 1995, Baak-Baak et al. 2013, Afify and Galizia 2014). These contradictions could be due to the use of different testing methodologies, rearing conditions, or the presence of background odors.

We aimed at citing all studies in which the same cue was tested without judging their relative importance, and suggest referring to the original studies in order to evaluate contradictory results (the latest search for this review was done on 31 July 2014). We discussed some open questions regarding the interactions between the different cues and whether the response to these cues is innate or shaped by experience according to the available literature.

Cues From Larval Food

Plant detritus and the microorganisms that live on it in water are food sources for most mosquito larvae (Merritt et al. 1992), and affect mosquito larvae growth rates (Yee et al. 2007, Murrell and Juliano 2008, Kesavaraju et al. 2009). A number of studies have evaluated cues from plant (Table 1) and microbial (Table 2) origins on mosquito oviposition. Infusions of white oak,

Table 2. Cues of microbial origin and their effect on the oviposition of different mosquito species

Cue	Attractant	Repellent	Stimulant	Deterrent
Microbes				
Bacteria isolated from white oak leaf infusion			*Ae. aegypti*[1]	
Bacteria isolated from bamboo (*Arundinaria gigantea*) leaf infusion			*Ae. aegypti*[1]	
Bacteria isolated from bamboo (*Bambusa* spp.) leaf infusion			*Ae. aegypti*[2]	
Bacteria isolated from alfalfa hay infusion	*Cx. quin.*[3]		*Cx. quin.*[3]	
Bacteria isolated from natural mosquito habitats	*A. gambiae*[4]			
Bacillus sp. (from oak leaf infusion)			*Ae. albopictus*[5]	
Psychrobacter immobilis (from larval water)			*Ae. albopictus*[5]	
Mixed cultures of bacteria from larval habitat (*Stenotrophomonas*, *Enterobacter*, *Pantoea*, *Klebsiella*, *Acinetobacter*, *Aeromonas*, *Pseudomonas*, *Bacillus*)				*A. gambiae*[6]
Sphingobacterium multivorum (from soil)			*Ae. albopictus*[5]	
Culture of *Bacillus sphaericus*			*Cx. quin.*[7]	*Cx. quin.*[8]
Bacillus thuringiensis var *israelensis*			*Ae. albopictus*[9] *Cx. quin.*[7]	*Cx. quin.*[8]
Compounds from microbes				
Secondary metabolites of *Trichoderma viride*			*Cx. quin.*[10]	
Compounds associated with bacteria in bamboo leaf infusion (nonanoic acid, tetradecanoic acid, tetradecanoic acid methyl ester)			*Ae. aegypti*[1]	
A synthetic mixture of nonanoic acid, tetradecanoic acid, and tetradecanoic acid methyl ester			*Ae. aegypti*[1,11]	*Ae. aegypti*[1]
A compound associated with bacteria in bamboo leaf infusion (hexadecanoic acid methyl ester)				*Ae. aegypti*[1]

Citations: [1] (Ponnusamy et al. 2008), [2] (Arbaoui and Chua 2014), [3] (Hazard et al. 1967), [4] (Sumba et al. 2007), [5] (Trexler et al. 2003b), [6] (Huang et al. 2006), [7] (Barbosa et al. 2007), [8] (Zahiri and Mulla 2005), [9] (Carrieri et al. 2009), [10] (Geetha et al. 2003), [11] (Barbosa et al. 2010a).

Ae., *Aedes*; *Cx.*, *Culex*; *Cx. quin.*, *Culex quinquefasciatus*; *A.*, *Anopheles*.

Bermuda grass, and bamboo (McPhatter and Debboun 2009; Obenauer et al. 2010; Ponnusamy et al. 2010a,b), or chemical compounds isolated from these infusions (3 methylindole and nonanal; Millar et al. 1992, Du and Millar 1999) were found to be stimulants and attractants for one or more mosquito species. Microbes isolated from plant infusions (like *Bacillus sp.* isolated from oak leaf infusion) also stimulate and attract mosquito oviposition (Hazard et al. 1967, Trexler et al. 2003b, Ponnusamy et al. 2008). Importantly, other factors also influence the attractiveness of infusions, such as the mass of plant material, fermentation period (Ponnusamy et al. 2010b), and the diversity of microbial species (Ponnusamy et al. 2010a).

Other plants (such as *Solenostemma argel Delile*) have a negative effect on mosquito eggs (Al Doghairi et al. 2004, Elango et al. 2009, Warikoo et al. 2011) or larvae (Al Doghairi et al. 2004, Rajkumar and Jebanesan 2009). Not surprisingly, these plants were found to be deterrent for mosquito oviposition (Al Doghairi et al. 2004, Elango et al. 2009, Rajkumar and Jebanesan 2009, Warikoo et al. 2011), showing that mosquitoes avoid conditions that are noxious to their offspring. However, suitability for the offspring does not always explain the oviposition effect of plant infusions; the water soluble lectin isolated from the *Moringa oleifera Lamarck* tree is larvicidal and ovicidal against *Ae. aegypti* (Coelho et al. 2009, Santos et al. 2012), but stimulates oviposition in this species (Santos et al. 2012). No explanation for this counterintuitive effect is as yet known.

Some oviposition responses are experience dependent. *Cx. quinquefasciatus* larvae reared in water containing an innately deterrent concentration of 3 methylindole subsequently preferred water containing the same concentration of 3 methylindole over the normally attractive *p* cresol (McCall and Eaton 2001). Learning that is transferred through metamorphosis (McCall and Eaton 2001) may be insufficient, and additional enforcement at the early adult stage may be necessary (Hamilton et al. 2011).

Cues From Mosquito Immature Stages

The current or previous presence of a low density of other mosquitoes in the water (i.e. eggs, larvae, and pupae) could encourage conspecific mosquitoes to use the same site (Soman and Reuben 1970, Trimble and Wellington 1980, Wachira et al. 2010, Wong et al. 2011). Pheromones from immature stages that stimulate their conspecifics to lay eggs have been identified (Mboera et al. 2000a,b; Mendki et al. 2000; Ganesan et al. 2006; Seenivasagan et al. 2009). However, high densities of mosquito immature stages in water generate competition, with negative effects on larvae and the emerging adults (Ho et al. 1989, Reiskind and Lounibos 2009). Indeed, water that contains high numbers of immature stages (Zahiri and Rau 1998) or high dose of their pheromones (Barbosa et al. 2007, Seenivasagan et al. 2009) is deterrent and repellent for the oviposition of their conspecifics. This means that mosquitoes evaluate not only the presence of conspecifics but also their density. Similarly, water that contains starved larvae (Zahiri and Rau 1998) or larvae that are infected with pathogens (Zahiri and Rau 1998, Zettel Nalen et al. 2013) also deter egg laying of conspecifics,

Table 3. Cues of mosquito immature stages and their effect on the oviposition of different mosquito species

Cue	Attractant	Repellent	Stimulant	Deterrent
Water with immature stages				
With *Ae. triseriatus* eggs				*Ae. triseriatus*[1]
With *Cx. quin.* eggs	*Cx. quin.*[2] *A. gambiae*[2]	*A. gambiae*[2]	*Cx. quin.*[3]	
With *Ae. albopictus* eggs			*Ae. albopictus*[4]	*Ae. albopictus*[4]
With *Ae. albopictus* larvae			*Ae. albopictus*[4]	
With *Cx. quin.* larvae	*Cx. quin.*[2]	*A. gambiae*[2]	*Cx. quin.*[5]	
With *O. australis* larvae			*O. australis*[5]	
With *Ae. togoi* larvae			*Ae. togoi*[6]	
With *Ae. atropalpus* larvae			*Ae. aegypti*[7] *Ae. atropalpus*[7]	
With *Ae. aegypti* larvae			*Ae. aegypti*[7,8,9]	
With *Ae. aegypti* pupae			*Ae. aegypti*[8,9]	
Compounds extracted from immature stages				
Material associated with *Cx. tarsalis* eggs			*Cx. tarsalis*[10]	
Apical droplet material of *Culex* egg rafts			*Cx. quin.*[11] *Cx. tarsalis*[11]	
Pheromone of *Cx. quinquefasciatus* eggs (erythro-6-acetoxy-5-hexadecanolide)	*Cx. quin.*[12]		*Cx. quin.*[3,12 20] *Cx. cinereus*[13] *Cx. pipiens molestus*[21]	*Cx. quin.*[16]
Pheromone of *Ae. aegypti* larvae (*n*-heneicosane)	*Ae. aegypti*[22]	*Ae. aegypti*[22]	*Ae. albopictus*[23] *Ae. aegypti*[22,24,25]	*Ae. albopictus*[23] *Ae. aegypti*[22]
Compounds extracted from *Ae. aegypti* eggs (dodecanoic acid and tetradecanoic acid)			*Ae. aegypti*[26,27] *Cx. quin*[27]	
Compounds extracted from immature stages (*Ae. aegypti* eggs)				
(Z)-9-Hexadecenoic acid			*Ae. aegypti*[26]	
(Z)-9-Octadecenoic acid, methyl dodecanoate, methyl tetradecanoate, methyl (Z)-9-hexadecenoate, methyl hexadecanoate, methyl (Z)-9-octadecenoate, and methyl octadecanoate				*Ae. aegypti*[26]
Octadecenoic acid			*Ae. aegypti*[26]	*Ae. aegypti*[26]
Hexadecanoic acid			*Ae. aegypti*[27] *Cx. quin*[27]	*Ae. aegypti*[26]
Water with immature stages at harsh conditions				
Ae. aegypti larvae infected with the microsporidian pathogen *Edhazardia aedis*				*Ae. aegypti*[28]
Ae. aegypti larvae killed mechanically or by *Tox. theobaldi* predation			*Ae. aegypti*[29]	
Water previously contained larvae at harsh conditions				
Ae. aegypti crowded or starved larvae				*Ae. aegypti*[30,31]
Ae. aegypti larvae infected with the parasite *Plagiorchis elegans*				*Ae. aegypti*[7,30 33]
Ae. atropalpus larvae infected with the parasite *Plagiorchis elegans*				*Ae. aegypti*[7] *Ae. atropalpus*[7]
Ae. aegypti larvae infected with the gregarine *Ascogregarina taiwanensis*			*Ae. aegypti*[34]	
Ae. aegypti larvae infected with the symbiotic yeast *Candida* near *pseudoglaebosa*			*Ae. aegypti*[34]	

Citations: [1] (Kitron et al. 1989), [2] (Wachira et al. 2010), [3] (Braks et al. 2007), [4] (Wasserberg et al. 2014), [5] (Mokany and Shine 2003), [6] (Trimble and Wellington 1980), [7] (Zahiri et al. 1997a), [8] (Soman and Reuben 1970), [9] (Wong et al. 2011), [10] (Osgood 1971), [11] (Bruno and Laurence 1979), [12] (Mboera et al. 2000a), [13] (Mboera et al. 1999), [14] (Blackwell et al. 1993), [15] (Olagbemiro et al. 1999), [16] (Barbosa et al. 2007), [17] (Mboera et al. 2000b), [18] (Olagbemiro et al. 2004), [19] (Dawson et al. 1990), [20] (Laurence and Pickett 1982), [21] (Michaelakis et al. 2005), [22] (Seenivasagan et al. 2009), [23] (Gonzalez et al. 2014), [24] (Mendki et al. 2000), [25] (Baak-Baak et al. 2013), [26] (Ganesan et al. 2006), [27] (Sivakumar et al. 2011), [28] (Zettel Nalen et al. 2013), [29] (Albeny-Simoes et al. 2014), [30] (Zahiri and Rau 1998), [31] (Zahiri et al. 1998), [32] (Lowenberger and Rau 1994), [33] (Zahiri et al. 1997b), [34] (Reeves 2004).

Ae., *Aedes*; *Cx.*, *Culex*; *Cx. quin.*, *Culex quinquefasciatus*; *A.*, *Anopheles*; *O.*, *Ochlerotatus*.

suggesting that other compounds could be released from unhealthy larvae and inhibit oviposition of their conspecific gravid females.

Cues of mosquito immature stages could also affect oviposition of nonconspecific gravid females; *Anopheles gambiae* Giles gravid females prefer water with low density of *Cx. quinquefasciatus* eggs, and avoid water with high density of *Cx. quinquefasciatus* eggs or any densities of *Cx. quinquefasciatus* larvae (Wachira et al. 2010). The pheromone released by *Cx. quinquefasciatus* eggs stimulates egg laying of *Culex cinereus Theobald* (Mboera et al. 1999) and *Culex pipiens L.* (Michaelakis et al. 2005), suggesting a general oviposition stimulant effect on *Culex* mosquitoes.

In nature, cues of most mosquito immature stages are not present in clean water but rather in water that contains other cues (e.g. plant detritus), and these signals may interact. Indeed, a mixture of erythro 6 acetoxy 5 hexadecanolide (a pheromone of *Cx. quinquefasciatus* eggs) with grass infusion

Table 4. Cues of mosquito predators and their effect on the oviposition of different mosquito species

Cue	Attractant	Repellent	Stimulant	Deterrent
Water with a predator				
Gambusia affinis				*Cx. tarsalis*[1]
Betta splendens				*Ae. aegypti*[2]
Notonecta maculata				*C. longiareolata*[3,4]
Mesocyclops longisetus			*Ae. aegypti*[5]	
Anax imperator				*C. longiareolata*[6]
Anisops debilis			*O. caspius*[7]	*C. longiareolata*[7] *O. caspius*[7]
Water with predator cues (water previously contained a predator)				
Gambusia affinis				*Cx. quin.*[8] *Cx. tarsalis*[8] *Cx. pipiens complex*[9]
Notonecta maculata				*C. longiareolata*[4,10]
Eretes griseus				*Cx. tritaeni.*[11]
Mesocyclops longisetus			*Ae. aegypti*[5]	
Compounds released by a predator				
n-Heneicosane and *n*-tricosane (from *Notonecta maculata*)				*C. longiareolata*[10]

Citations: [1] (Walton et al. 2009), [2] (Pamplona et al. 2009), [3] (Blaustein 1998), [4] (Blaustein et al. 2004), [5] (Torres-Estrada et al. 2001), [6] (Stav et al. 1999), [7] (Silberbush et al. 2014), [8] (Van Dam and Walton 2008), [9] (Angelon and Petranka 2002), [10] (Silberbush et al. 2010), [11] (Ohba et al. 2012).

Ae., *Aedes*; *Cx.*, *Culex*; *Cx. quin.*, *Culex quinquefasciatus*; *Cx. tritaeni.*, *Culex tritaeniorhynchus*; *C.*, *Culiseta*; *O.*, *Ochlerotatus*.

encouraged oviposition more than the pheromone or the infusion alone (Mboera et al. 1999). A synergistic effect was also shown for this pheromone with the plant derived oviposition attractant 3-methylindole (Olagbemiro et al. 2004).

Cues From Mosquito Predators

Predators in water reduce mosquito larval populations (Blaustein 1998, Pyke 2005). Intuitively, gravid females may avoid laying eggs on water that contains predator cues (Table 4). Indeed, cues from the mosquito fish *Gambusia affinis* Gaird & Girard (Angelon and Petranka 2002, Van Dam and Walton 2008), the dragonfly predator *Anax imperator* Leach (Stav et al. 1999), and the hemipteran predator *Notonecta maculata* Fabricius (Blaustein et al. 2004) were found deterrent for mosquito oviposition. Furthermore, two compounds (*n*-heneicosane and *n*-tricosane) released by *N. maculata* induce oviposition avoidance in *Culiseta longiareolata* Macquart (Silberbush et al. 2010).

Responses toward predator cues are species specific. They may be partly genetically encoded and partly experience dependent. *Cx. quinquefasciatus* and *Cx. tarsalis* experience high predation by *G. affinis* in nature and avoid laying eggs in containers with predator cues, while *Ae. aegypti* has low risk of predation by *G. affinis* in nature and shows no oviposition avoidance behavior (Van Dam and Walton 2008). Similarly, the wetland mosquito *Culex tritaeniorhynchus* Giles avoids cues of the predacious beetle *Eretes griseus* Fabricius, while *Aedes albopictus* Skuse, which do not share the same habitat, are not affected by these cues (Ohba et al. 2012). An interesting case is given by *n*-heneicosane, the component released by *N. maculata* and responsible for its oviposition deterrent effect on *C. longiareolata* (Silberbush et al. 2010). For *Ae. aegypti* mosquitoes, this substance is an oviposition pheromone released from larval cuticle, and accordingly not deterrent (Mendki et al. 2000, Seenivasagan et al. 2009). The *n*-heneicosane is released by *Ae. aegypti* larvae which live in small containers. This is a very different habitat with different predation exposure than the pool environment inhabited by *N. maculata* (Silberbush et al. 2010). Mosquito species with no evolutionary experience with a predator have not evolved avoidance of water containing that predator or its chemical cues.

In an evolutionary arms race, the presence of a natural predator or its chemical cues could be undetectable or even attractant to its prey mosquitoes; the presence of the backswimmer predator *Anisops wakefieldi* White or its chemical cues had no effect on the oviposition of the prey mosquito *Culex pervigilans* Pergorth (Zuharah and Lester 2010). Interestingly, *Ae. aegypti* prefers to lay eggs in containers with its predacious copepod *Mesocyclops longisetus* Thiébaud or in containers that had *M. longisetus* for 48 hours, in a choice against clean water (Torres Estrada et al. 2001). *M. longisetus* is a voracious natural predator of *Ae. aegypti* larvae (Marten et al. 1994). It is not known why *Ae. aegypti* is attracted rather than repelled by its copepod predator.

Unlike the synergistic effects of plant derived substances and pheromones (see above), no interaction has been reported yet between food supply and predator presence. Oviposition of *Ae. albopictus* decreased with the presence of predator dragonfly nymphs and increased with the increase of food levels, but these effects were independent from each other (Wasserberg et al. 2013).

Synthetic Compounds

Several studies addressed the possibility of using synthetic compounds to influence mosquito oviposition (Table 5). Some of these compounds were first isolated and identified from plant infusions, bacterial cultures,

Table 5. Synthetic compounds and their effect on the oviposition of different mosquito species

Substance Ester compounds	Attractant	Repellent	Stimulant	Deterrent
Heptadecyl butanoate, pentadecyl hexanoate, tetradecyl heptanoate, tridecyl octanoate, butyl heptadecanoate				*Ae. albopictus*[1] *Ae. aegypti*[1] *A. stephensi*[2]
Octyl tridecanoate				*Ae. albopictus*[1] *Ae. aegypti*[1]
Undecyl decanoate			*A. stephensi*[2]	*Ae. albopictus*[1] *Ae. aegypti*[1] *A. stephensi*[2]
Decyl undecanoate, nonyl dodecanoate			*A. stephensi*[2]	*Ae. albopictus*[1] *Ae. aegypti*[1]
Dodecyl nonanoate			*A. stephensi*[2]	*Ae. aegypti*[1]
Octadecyl propanoate			*Ae. aegypti*[1]	*Ae. albopictus*[1] *A. stephensi*[2]
Hexyl pentadecanoate			*Ae. albopictus*[1]	*A. stephensi*[2]
Heptyl tetradecanoate				*Ae. albopictus*[1]
Propyl octadecanoate	*Ae. aegypti*[3] *A. stephensi*[3]		*Ae. aegypti*[1,3] *A. stephensi*[2,3]	*Ae. albopictus*[1]
Pentyl hexadecanoate			*A. stephensi*[2]	
Hexadecyl pentanoate		*Ae. albopictus*[4] *Ae. aegypti*[4] *A. stephensi*[4]		*Ae. albopictus*[1,4] *Ae. aegypti*[1,4] *A. stephensi*[2,4]
Ethyl 2-((4-nitrophenyl)diazenyl)-3-oxobutanoate	*Ae. aegypti*[5]		*Ae. aegypti*[5]	
Ethyl 2-((4-fluorophenyl)diazenyl)-3-oxobutanoate		*Ae. aegypti*[5]		*Ae. aegypti*[5]
Isobutyl 2-((4-fluorophenyl) diazenyl)-3-oxobutanoate		*Ae. aegypti*[5]		*Ae. aegypti*[5]
Methyl 2-((3-chlorophenyl)diazenyl)-3-oxobutanoate		*Ae. aegypti*[5]		*Ae. aegypti*[5]
Ethyl 2-((1-hydroxynaphthalen-2-yl)diazenyl)-3-oxobutanoate	*Ae. aegypti*[5]		*Ae. aegypti*[5]	
Mosquito host seeking repellents				
Diethyl m toluamide (DEET)			*Ae. aegypti*[6]	*Ae. albopictus*[6] *Cx. quin.*[6] *Ae. aegypti*[6 8]
Diethyl phenyl acetamide (DEPA)			*Ae. aegypti*[6]	*Ae. albopictus*[6] *Ae. aegypti*[6] *Cx. quin.*[6]
Diethyl benzamide (DEB)			*Ae. aegypti*[6]	*Ae. albopictus*[6] *Cx. quin.*[6]
1-(3-cyclohexen-1-ylcarbonyl)-piperidine, 1-(3-cyclohexen-1-ylcarbonyl)-2-methylpiperidine				*Ae. albopictus*[7]
Ethyl anthranilate (EA) and butyl anthranilate (BA)				*Ae. aegypti*[8]
A compound with no ecological significance				
Acetic acid			*Cx pipiens pallens*[9]	

Citations: [1] (Sharma et al. 2008), [2] (Sharma et al. 2009), [3] (Seenivasagan et al. 2012), [4] (Seenivasagan et al. 2010), [5] (Guha et al. 2012), [6] (Tikar et al. 2014), [7] (Xue et al. 2001), [8] (Afify et al. 2014), [9] (Li et al. 2009).

Ae., *Aedes*; *Cx.*, *Culex*; *Cx. quin.*, *Culex quinquefasciatus*; *A.*, *Anopheles*.

or mosquito immature stages (included in Tables 1, 2, or 3 for convenience). Ester compounds are abundant in dipteran sex pheromones (Jacobson et al. 1973), and also received an interest as potential oviposition cues. Some ester compounds were found to stimulate/attract mosquito oviposition while others were oviposition deterrents/repellents (Sharma et al. 2008, 2009; Seenivasagan et al. 2010, 2012; Guha et al. 2012). Synthetic compounds may resemble natural compounds that are present in the animal's ecological environment, but for some (including some known repellents that affect host seeking), no ecological significance is known (Li et al. 2009, Tikar et al. 2014).

Conclusion

In this review, we collect available information about substances that either increase or decrease oviposition in different species. The data are reported in Tables 1 5, and sorted by origin of the substances studied. What is apparent in the tables is that our knowledge is quite partial indeed: some species are well studied for many substances, and some substances for many species. But in most cases, knowledge is partial. It is important to emphasize these shortcomings, because the data also show that the same substance can have very different effect depending on the experimental conditions and on the species used. We hope that our collection will be of use to the community in designing future experiment to study mosquito behavior, and to design suitable approaches for environmentally friendly mosquito control strategies.

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