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REVIEW ARTICLE

Mosquito Attractants

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Abstract

Vector control and personal protection against anthropophilic mosquitoes mainly rely on the use of insecticides and repellents. The search for mosquito-attractive semiochemicals has been the subject of intense studies for decades, and new compounds or odor blends are regularly proposed as lures for odor-baited traps. We present a comprehensive and up-to-date review of all the studies that have evaluated the attractiveness of volatiles to mosquitoes, including individual chemical compounds, synthetic blends of compounds, or natural host or plant odors. A total of 388 studies were analysed, and our survey highlights the existence of 105 attractants (77 volatile compounds, 17 organism odors, and 11 synthetic blends) that have been proved effective in attracting one or several mosquito species. The exhaustive list of these attractants is presented in various tables, while the most common mosquito attractants - for which effective attractiveness has been demonstrated in numerous studies – are discussed throughout the text. The increasing knowledge on compounds attractive to mosquitoes may now serve as the basis for complementary vector control strategies, such as those involving lure-and-kill traps, or the development of mass trapping. This review also points out the necessity of further improving the search for new volatile attractants, such as new compound blends in specific ratios, considering that mosquito attraction to odors may vary over the life of the mosquito or among species. Finally, the use of mosquito attractants will undoubtedly have an increasingly important role to play in future integrated vector management programs.

Key Words Mosquito · volatile · attractant · compound · host odor

Introduction

Mosquitoes are responsible for the transmission of widespread and sometimes deadly infectious diseases, including malaria, chikungunya, dengue, and Zika. A great number of research projects have focused on methods to control vector-borne diseases by preventing people from being bitten by mosquitoes, such as the use of insecticides or repellents (Dye-Braumuller et al. 2020). For example, insecticide-treated nets (ITNs) and indoor residual spraying (IRS) of insecticides have been shown to limit vector-human contacts, although insecticide resistance threatens these strategies (Liu 2015). Repellents have been used so far mainly for personal protection against biting vectors. The use of repellents has also proved effective in reducing disease transmission by blocking contact between anthropophilic blood-sucking mosquitoes and human hosts (Debboun and Strickman 2013). The development of new bio-sourced mosquito repellents opens perspectives for more eco-friendly disease control (Grison et al. 2020). In parallel, novel promising strategies identify the potential of spatial repellents for disease prevention at the community level (Norris and Coats 2017).

In addition to the use of biocides, vector control and personal protection against anthropophilic mosquitoes may also rely on the use of trapping methods, in which target mosquitoes are attracted to and caught in specifically designed odor-baited traps (Achee et al. 2019). For example, the recent rapid expansion of the invasive mosquito *Aedes albopictus*, which has colonized every continent and many countries in the past 30 years (Bonizzoni et al. 2013; Paupy et al. 2009), raised an emerging risk for public health (*Ae. albopictus* is the main vector of several viruses). This mosquito is also an important source of nuisance for urban populations. This context has led to an increasing number of studies devoted to the development of new trapping techniques against this species, including

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attempts to use mosquito-attractive lures to control it (Akhoundi et al. 2018; Roiz et al. 2016). Moreover, improving the efficacy of trapping methods has several scientific and practical purposes. It would support local survey of mosquito species and their population abundance, surveillance of invasive mosquito species, monitoring of vector-borne pathogens, and prediction of disease epidemics (Akhoundi et al. 2018; Englbrecht et al. 2015). Mosquito attractants may thus play a key role in future programs of integrated vector management for the control and surveillance of mosquitoes. The use of attractants may help reduce the use of insecticides in coming years (Mafra-Neto and Dekker 2019; Mweresa et al. 2020).

The efficacy of trapping methods depends upon both the trapping device and the use of effective mosquito attractants. Many trapping devices (types of traps) are now available and have been already evaluated in numerous comparative studies for different mosquito species (Bazin and Williams 2018; Kline 2006; Thornton et al. 2016). Regarding mosquito-attractive compounds, many studies have already investigated how mosquitoes locate and choose their host, or are guided towards plants, and have reported numerous chemical compounds that are attractive to mosquitoes. As host location in blood-sucking insects is known to be mostly mediated by olfactory cues (Syed 2015; Takken and Knols 1999; Takken and Knols 2010), the key role of vertebrate host odors has been particularly investigated in anthropophilic mosquitoes that transmit pathogens to humans (e.g. *Anopheles*: Meijerink et al. 2000; Takken and Knols 1999; *Culex*: Syed and Leal 2009; *Aedes*: Dekker et al. 2005; Logan et al. 2008. Together with attraction to host odors, adult mosquitoes are guided by olfaction towards many other volatile compounds, at all stages of their biological cycle: mating, oviposition, or sugar-feeding on plants (Bentley and Day 1989; Foster and Takken 2004a; Mozūraitis et al. 2020; Nyasembe and Torto 2014; Vaníčková et al. 2017). Consequently, many volatile compounds, blends of compounds, or natural odor extracts are already used today for the trapping of different mosquito species (Wooding et al. 2020). However, the use of attractants for mosquito surveillance and control remains empirical and the precise conditions of efficacy are so far undefined.

Classifying a compound as a "mosquito attractant" requires a proper verification of the compound's properties and its attractive effects. Particularly, some of the following points must be addressed when evaluating the attractiveness of a compound: (i) its specificity concerning different mosquito species and non-target insects, (ii) its specificity with regard to specific physiological stage and sex (immature stages, sugar-feeding adults, host-seeking females, breeding site location), (iii) the relative contribution of the compound to the attractiveness when presented individually or in combination with other compounds, (iv) the effect of the dose on the valence of the tested compound, and the possible existence and activity of isomeric forms of the compound.

Although mosquito-attractant volatiles have been the object of intensive study for more than a century, and have been the subject of several reviews (Mwingira et al. 2020; Smallegange and Takken 2010; Sukumaran 2016; Takken 1991; Takken and Knols 1999; Wooding et al. 2020), new attractive molecules or odor blends are regularly investigated as mosquito lures, and particular developments have been proposed over the last decade. A first complete list of attractive compounds was established by Smallegange and Takken (2010), for the three main mosquito species of importance to human health, *Aedes aegypti*, *Anopheles gambiae,* and *Culex quinquefasciatus*. More recently, Wooding et al. (2020) proposed an updated list of the main semiochemicals mediating different stages of adult mosquito life, mating, oviposition, host-seeking, and sugar-feeding, in 11 mosquito species.

The present review aims to substantially supplement these data by providing a comprehensive list of all the compounds, blends of molecules, or natural odors that have been successfully evaluated for mosquito attractiveness. In this paper, the term "attractant" is used in the sense defined by Dethier et al. (1960), although other definitions have been proposed afterwards (Plimmer et al. 1982), as "a chemical which causes insects to make oriented movements towards its source". We considered in this review all compounds that were demonstrated to be attractive to mosquitoes in the light of laboratory behavioural assays (such as in olfactometer or wind tunnel) or under field conditions (by using diverse trapping methods). The goal of this review is to gather for each attractant a list of studies, methods used, compounds tested in combination, and effects on different mosquito species. We used a chemical approach, in which the classification was based on the name of compounds (instead of listing the compounds per mosquito species). This gives a simple view of the attractive effect of each compound/odor and the range of its biological activity and allows easy comparison of its effects on different mosquito species, including those less frequently studied. Presenting the effects by type of chemical, rather than by mosquito species, allows a quick census of all the studies performed with a particular compound on any mosquito species.

We first propose, in section 1, a brief historical view of the discovery of mosquito attractants throughout the last 100 years. In section 2, we detail the methods used in constructing the list of attractants. Section 3 presents the full list of known mosquito attractants. Then, in section 4, we propose future directions in the study of mosquito attractants.

History of the Discovery of Mosquito Attractants

At the beginning of the 20th century, odors were not considered to play any role in mosquito attraction. Temperature was first imagined as the main attractive cue for these insects:

mosquitoes were held to detect the presence of living warm-blooded animals by their attraction to the « warm air rising from hot surfaces » (Howlett 1910). This author verified the effect of heat by placing adult mosquitoes in a gauze bag close to a tube full of hot water, and reported movements and aggregation of *Aedes (Stegomyia) scutellaris* mosquitoes that proved the role of the hot air. Regarding the role of smell, he concluded that « blood and sweat have no apparent influence ». Other authors also proposed that heat was attractive to mosquitoes, such as Crumb (1922) . This author also recorded an effect of breath on mosquito activation but excluded carbon dioxide as a possible attractant. In the same year, Rudolfs (1922) was the first to hypothesize that « CO_2 produced by breathing is the initial attractive agent for the mosquitoes ». He also suggested that other compounds such as ammonia, benzoic acid and some amino acids might be attractive to *Aedes* species. Laboratory tests using cow or pig blood showed that blood enhanced mosquito attraction (Burgess and Brown 1957; Reuter 1936; Van Thiel and Weurman 1947). Among the constituents of blood likely responsible for this effect, it was long thought that blood is attractive because it contains CO_2 « transpired through the skin from the cutaneous capillaries » (Burgess and Brown 1957; Van Thiel 1937). However, excretion of carbon dioxide through the skin was later considered as too low to play a role in this way, and human breath sources of CO_2 were then found to play a major role in mosquito attraction (Brouwer 1960; Gillies 1980). Carbon dioxide was then rapidly proved to be highly effective for catching mosquitoes during field trapping campaigns (Brown 1951; Headlee 1934; Huffaker 1942; Huffaker and Back 1943; Reeves 1951; Van Thiel and Weurman 1947).

Haddow (1942) was the first to test human odors in behavioural assays, and found that the presence of unwashed children within huts allowed catching many more mosquitoes compared to huts with washed children inside. Such preferences were found for *An. gambiae*, *An. funestus*, *An. pharoensis*, *Taeniorhynchus africanus* and *T. uniformis*, and similar results were obtained when children were replaced by clothes they had worn. Haddow suggested that the « attractant powers of the various constituents of sweat » be further explored. A few years later, Willies (1947) used an experimental dual-port olfactometer to show that mosquito species such as *Ae. aegypti* and *An. quadrimaculatus* were strongly attracted to the odor from a human arm. At the same period, similar experiments conducted by Parker (1948) , Ribbands (1949) , Muirhead-Thomson (1951a, b), Thompson and Brown (1955) , and later by Mayer and James (1969) and Price et al. (1979) , confirmed the primary importance of human odors for mosquito attraction. Nonetheless, few authors still considered skin odors (Wright 1962, 1975) or human sweat (Brown 1966) to have an obvious role in mosquito attraction.

The use of human odor extracts as bait for mosquito traps was developed only in the 1990s.

Following observations that feet are the preferred biting sites for the main human malaria vectors in Africa, *An. gambiae* and *An. arabiensis* (De Jong and Knols 1995; Dekker and Takken 1998), foot odors have been suspected to be highly attractive to anthropophilic mosquitoes. Njiru et al. (2006) showed that traps baited with nylon socks worn by human subjects were very efficient for catching adult mosquitoes under field conditions. Other authors then successfully used traps baited with nylon socks to collect mosquitoes (Jawara et al. 2009; Qiu et al. 2006b; Schmied et al. 2008; Smallegange et al. 2010).

Before the first detailed analyses of the chemical composition of human body odors, and particularly skin and sweat volatiles, in the early 2000s (reviewed by Dormont et al. 2013), some authors investigated the possible role of isolated compounds already known to be produced by sweat. Among these molecules, the effect of lactic acid on mosquito behavior was investigated very early, by Rudlofs (1922). This author found a repellent effect of lactic acid, and further studies also found this compound to be either repellent or neutral to different mosquito species (Brown et al. 1951; Reuter 1936; Schaerffenberg and Kupka 1959; Skinner et al. 1968). The high concentrations tested in these studies may explain the contradiction between their results and those of other studies showing lactic acid to be an attractant at more relevant concentrations (Acree et al. 1968). Indeed, Miiller (1968) showed that the valence of L-lactic acid changes from repellence to attraction depending on concentration. The attractant effect of lactic acid was later confirmed by other laboratory bioassays (Dekker et al. 2002; Smallegange et al. 2005; Smith et al. 1970) and by physiological studies (Davis and Sokolove 1976). Lactic acid has been successfully used for baited-traps in the field, though often in combination with other attractants (Hoel et al. 2007; Jawara et al. 2011; Kline et al. 1990a).

Ammonia is another molecule targeted by early investigations of possible attractant. Both Rudolfs (1922) and Reuter (1936) conducted tests with ammonia on *Aedes* and *Anopheles* species, but found this compound little (or not at all) attractive. Later, Brown (1951) and Rössler (1961) tested ammonia for the attraction of *Ae. aegypti*, but also concluded that this compound did not affect mosquitoes. Geier et al (1999a) were the first to suspect synergistic effects with lactic acid, and demonstrated that ammonia was actually an attractive compound for *Ae. aegypti* when combined with lactic acid. Physiological activity of mosquito antennae to ammonia has subsequently been shown by Meijerink et al. (2001) , and ammonia has been added to the list of attractant components for baited-traps in the field (Jawara et al. 2011; Njiru et al. 2006).

Carboxylic acids were also early suspected to play a role in mosquito attraction. The effects of compounds such as benzoic, formic, propionic, butyric, and caproic acids were examined by Rudolfs (1922) and Reuter (1936), and later by Delong et al. (1949) and Brown et al. (1951). However, these studies did not show any attractant effect of these compounds on mosquitoes. In 1973, Carlson et al. were the first to show the attractant effect to *Ae. aegypti* of several 2C-5C carboxylic acids in an olfactometer. Later, several studies showed physiological and behavioral activities of diverse short- and medium-chain carboxylic acids for *An. gambiae* and *Ae. aegypti* (Cork and Park 1996; Knols et al. 1997; Meijerink and van Loon 1999; Pappenberger et al. 1996) and carboxylic acids have thus been used in baited-traps experiments (Jawara et al. 2011; Smallegange et al. 2009).

The mosquito-attractant effect of another compound, 1-octen-3-ol (hereafter "OCT"), now often used in baited-traps, was shown by Takken and Kline (1989) . The role of this compound as an insect attractant was first mentioned by Buttery and Kamm (1980), who found that a volatile compound from alfalfa (*Medicago sativa*), OCT, could be likely responsible for the attraction of the major pest, the alfalfa seed chalcid. Hall et al. (1984) discovered the attractiveness of OCT to tsetse flies by investigating the olfactory stimulants from cattle odors by electroantennography (EAG). Takken and Kline (1989) were the first to show the efficacy of OCT as a mosquito attractant, used individually in baited-traps or synergistically with CO_2, and this compound is now often used in bait traps during field experiments (Cooper et al. 2004; Kline and Mann 1998; Rueda et al. 2001; Shone et al. 2003; Vythilingam et al. 1992).

Since the early 2000s, several new mosquito traps, developed either for scientific use or a commercial purpose, have been designed and tested under field conditions. Most of them rely on the use of synthetic olfactory lures, consisting of specific blends of volatile compounds shown to attract mosquitoes in previous studies. Several synthetic blends (see chapt. 4 for details) have been formulated and used as baits for mosquito-trapping devices. The lures usually consist of a mixture of a few compounds, including often lactic acid, ammonia, and carboxylic acids, e.g. the USDA blend (Bernier et al. 2001), the BG-lure (Geier et al. 2004a, b), the Ifakara blend (Okumu et al. 2010a), or the Mbita blend (Mukabana et al. 2012b).

Although the role of skin microorganisms in the production of body odors has long been known (Shelley et al. 1953), and the influence of microbiota on skin attractiveness to mosquitoes was early suggested by Schreck and James (1968), the effect of skin compounds of bacterial origin on mosquito behaviour has been only studied since the 1990's. De Jong and Knols (1995) observed a significant decrease in the attractiveness of feet to mosquitoes when they were washed with an antibacterial agent. Later, the same team documented the responses of mosquitoes to diverse volatiles of bacterial origin extracted from Limburger cheese (Knols et al. 1997), while other authors investigated the possible role of skin microbiota present in human sweat on mosquito behaviour (Braks et al. 1999, 2000; Braks and Takken 1999). The influence of microorganisms on mosquito attraction is now clearly established (Verhulst et al. 2010a, 2009, 2011a, b).

Literature Search and Data Extraction

As mentioned above, we considered in this review all chemicals that were demonstrated to be attractive to mosquito species, based on laboratory behavioural assays or field trapping experiments. Studies that investigated compounds only through electrophysiology (electroantennography, single sensillum recording, calcium imaging, …) were excluded from this review. These methods examine antennal detection by mosquitoes but do not evaluate the effective attractiveness of a compound, which requires behavioural assays. We took into account only those electrophysiology experiments that aimed at understanding the underlying mechanisms of attraction by compounds shown to be active in behavioural tests.

We reviewed the different types of volatile chemical cues used by mosquitoes in various contexts of adult mosquito life, such as odors involved in sugar-feeding, host-finding cues, and odors guiding gravid females towards oviposition sites. Volatiles involved in mating, such as sex pheromones, have been well covered in recent detailed reviews (Pitts et al. 2014; Vaníčková et al. 2017; Wooding et al. 2020) and were not included in our study.

Our bibliographic database was elaborated by searching published articles containing the terms "mosquito" AND "attractant" OR "odor" OR "volatile" OR "host" OR "behaviour" OR "trap" OR "semiochemicals". Literature searches were conducted using PubMed and Web of Science until June 2020. A total of 388 studies were included in this review, from which 316 studies experimentally evaluated the attractiveness of 105 compounds and odors (38 different mosquito species studied) (Tables 1 and 2), and 72 other studies tested or simply used synthetic attractive blends (Table 3).

As mentioned above, studies that employed only electrophysiological methods were not included in this review, nor were studies of pheromones and compounds identified to serve as chemical cues in mating. We also did not retain studies that only compared the efficiency of different trap types, in which trapping effectiveness was evaluated in the light of trap configuration (and without evaluating odor bait constituents).

For all included studies, we extracted the following data: names of the volatile compounds/odors and other compounds tested, names of target mosquito species, methods used to evaluate attractiveness, the effect of the compounds/odors on

Table 1 List of compounds attractive to adult mosquitoes. Compounds are given in alphabetical order, even for compounds whose name begins with a number. For each compound, studies and effect of the compound are given with respect to mosquito species, which are listed in alphabetical order. Studies that involved only electrophysiological methods (with no behavioural tests) were not included in this table. Studies that only compared the efficacy of different traps were also excluded from the table. For each compound, the column « co-tested compounds » gives the other compounds whose effects were tested in the study. The column « effect » indicates whether the compound was observed to be attractive alone (Attract.), attractive in combination/synergy with other compounds (Syn. (compound)), synergist for other compounds (Syn.of (compound)), not attractive (No effect), or repellent (Repellent).

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
Acetaldehyde	*C. quinq.*		Standard cage oviposition	Attract. (GF)	Choo et al. (2018)
6-acetoxy-5-hexadecanolide	*C. quinq.*	skatole, grass infusion	2W-olfactom., ovitraps, CDC, CFG, EAG	Attract. / Syn. (skatole)	Blackwell et al. (1993); Mboera et al. (2000b); Olagbemiro et al. (2004); Paiva et al. (2019)
Acetic acid	*Ae. aegypti*	CO_2, armpit sweat, AM, LA	2W-olfactom.	No effect	Brown et al. (1951)
		CO_2, LA, FAs, formic acid, OCT, 6M5H, other	2W-olfactom.	Attract.	Allan et al. (2006); Carlson et al. (1973); Müller (1968); Saratha and Mathew (2016)
Acetone	*Ae. aegypti*	CO_2	Flight tube, SSR	Attract.	Ghaninia et al. (2019)
		LA, DMDS + other compounds	Triple cage-2W-olfactom., field CDC-CFG-FP	Syn. (LA, DMDS)	Bernier et al. (2007); Bernier et al. (2003); Silva et al. (2005)
		Hand odor, hexanoic acid, BG-lure	Y-olfactom. + field BGS	Syn. (BG-lure)	Williams et al. (2006a)
		LA, butanone, AM, cyclopentanone	2W-olfactom.	Syn. (LA + butanone)	Venkatesh and Sen (2017)
	Ae. albopictus	LA, hand odor	Wind T.	Syn. (LA)	Hao et al. (2012)
		CO_2, OCT, DMDS + other compounds	Field MMX	No effect	Cilek et al. (2012)
	An. arabiensis	CO_2, LA, human odor, other compounds	Field Obet, CDC, sticky traps	No effect	Hawaria et al. (2016); Torr et al. (2008)
	An. coluzzii	CO_2	Flight tube, SSR	Repellent	Ghaninia et al. (2019)
	An. gambiae	LA, AM, OCT + other compounds	2W-olfactom., wind T.	CO_2 or LA	Qiu et al. (2011); Takken et al. (1997)
	C. nigripalpus	LA, DMDS, 1-hexen-3-ol, OCT, other compounds	Triple cage-2W-olfactom. + Field MMX	Syn. (LA, hexenol, OCT)	Bernier et al. (2003); Kline et al. (2012)
	C. quinq.	LA + other compounds	Triple cage-2W-olfactom. + Field MMX	Syn. (LA)	Bernier et al. (2003); Cilek et al. (2012)
		CO_2, foot odor, butyric acid, OCT	Field CFG-CDC	No effect	Mboera et al. (2000c)
Ammonia	*Ae. aegypti*	CO_2, LA, acetic acid, armpit sweat	2W-olfactom.	No effect	Brown et al. (1951)
		CO_2, LA, FAs, skin extracts, hand odor	Y-olfactom.	Syn. (LA)	Bosch et al. (2000); Geier et al. (1999a); Geier et al. (2002); Williams et al. (2006b)
		CO_2, LA, FAs, OCT, terpenes…	2W-olfactom.	Attract.	Mathew et al. (2013)
	Ae. albopictus	LA, DMDS, hexanoic acid, ethyl butyrate, OCT, 6-methyl-5-hepten-2-one	Y-olfactom. + field traps	Syn. (LA)	Wang et al. (2020)
		Mix-5, BG-lure, LA, hexanoic acid, 3-methyl-1-butanol, cyclopentanone, 6M5H, OCT	4A-olfactom. + field BGS	No effect	Xie et al. (2019)
	An. coluzzii	Foot odors	2W-olfactom.	Syn. (Foot odors more attractive)	De Boer et al. (2017)
		LA, TEA, butan-1-amine, 3-methyl-1-butanol, 3-methyl-butanoic acid, 3-methyl-butanoic acid, 3-methylbutanal	2W-olfactom.	Syn. (LA, TEA)	van Loon et al. (2015)
	An. gambiae	LA, TEA, other FA		Syn. (LA, TEA)	Jawara et al. (2011); Smallegange et al. (2012); Smallegange et al. (2009); Smallegange et al. (2005); Verhulst et al. (2010a)
		LA, TEA, 3-methyl-1-butanol, butan-1-amine	2W-olfactom. + field MMX	Syn. (LA, TEA, 3-methyl-1-butanol, butan-1-amine)	Menger et al. (2015); Menger et al. (2014a); Menger et al. (2014b); Mukabana et al. (2012b); Verhulst et al. (2011a)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		Foot odors, CO_2	2W-olfactom. + field MMX	Syn. (CO_2)	Njiru et al. (2006); Olanga et al. (2010); Spitzen et al. (2008); Verhulst et al. (2011b)
		Hand odors	2W-olfactom. + EAG	Syn. (LA. Human odors more attractive)	Qiu et al. (2006b); Smallegange et al. (2002); Smallegange et al. (2003)
		LA, sweat	2W-olfactom.	Attract.	Braks et al. (2001)
		LA, DMDS, 7-octenoic acid, 1-dodecanol, 6-methyl-5-hepten-2-one, GA, indole	2W-olfactom.	Syn. (LA. 7-octenoic increases)	Qiu et al. (2011)
	An. arabiensis	Foot odor (worn socks), cow urine	Odor-baited sticky trap	Syn. (CO_2, LA)	Hawaria et al. (2016)
	C. quinq.	Chicken feces	2W-olfactom. + EAG	No effect	Cooperband et al. (2008)
Anisaldehyde	*Ae. albopictus*	Human odor, linalool, geraniol, citronellal, eugenol, citral	Wind Tunnel	Attract.	Hao et al. (2013)
Benzaldehyde	*Ae. aegypti*	CO_2, FAs, other	2W-olfactom.	Syn. (Selected FAs)	Peach et al. (2019b)
	C. pipiens	Phenylacetaldehyde, (E)-2-nonenal, other	2W-flight olfactom.	Syn. (Phenylacetaldehyde + (E)-2-nonenal)	Otienoburu et al. (2012)
	C. pipiens pallens	OCT, hexanal, FAs, terpenes, other	Y-olfactom. + baited traps	Attract. / Syn. (OCT + hexanal + 2FAs)	Tian et al. (2018); Yu et al. (2015)
Benzothiazole	*An. gambiae*	Human odor	2W-olfactom.	Attract. long range / Repellent	Qiu et al. (2004)
Butan-1-amine	*An. coluzzii*	AM, LA, TEA, 3-methyl-1-butanol	2W-olfactom.	Syn. (AM, LA, TEA, 3-methyl-1-butanol)	van Loon et al. (2015)
	An. gambiae	AM, LA, TEA, 3-methyl-1-butanol	Flight chamber, MMX	Syn. (AM, LA, TEA, 3-methyl-1-butanol)	Menger et al. (2015); Menger et al. (2014a); Menger et al. (2014b); Mweresa et al. (2016)
Butanoic acid	*Ae. aegypti*	Tansy flowers odor, synthetic blend	2W-bioassays	Syn. (synth. Blend)	Peach et al. (2019b)
	Ae. albopictus	FAs: TEA, propanoic, hexanoic, + 14	Y-olfactom.	Attract.	Seenivasagan et al. (2014)
	An. gambiae	AM, LA, TEA, other	2W-olfactom., MMX, CDC	Attract.	Jawara et al. (2011); Smallegange et al. (2009)
Butanone	*Ae. aegypti*	Hand odor, 6M5H, other	3-cages-2W-olfactom., MMX	(Attract.)	Bernier et al. (2002)
		LA, acetone, AM, cyclopentanone	2W-olfactom.	Syn. (LA + acetone)	Venkatesh and Sen (2017)
	Ae. infirmatus, C. salinarius	CO_2, OCT	CDC	Syn. (CO_2)	Kline and Mann (1998)
	Ae. taeniorhynchus, A. atropos, C. nigripalpus, other	CO_2, OCT, LA, phenol	CDC	Repellent	Kline et al. (1990a)
Butyric acid	*Ae. aegypti*	OCT, 6M5H, FAs	2W-olfactom.	No effect	Saratha and Mathew (2016)
	Ae. japonicus japonicus	CO_2, FAs, DMDS, OCT, other	Field CDC	Syn. (OCT + propionic acid + valeric acid)	Anderson et al. (2012)
	C. quinq.	CO_2, acetone, OCT, foot odors	Field CFG, CDC	No effect	Mboera et al. (2000c)
Carbon dioxide	*Ae. aegypti*	-	Wind Tunnel	Attract.	Hoel et al. (2015); Jerry et al. (2017); Klun et al. (2013); Majeed et al. (2017); Majeed et al. (2014); van Breugel et al. (2015)
		LA	2W-olfactom. + Field trap	Attract.	Kusakabe and Ikeshoji (1990)
		LA, hand odor, arm odor, other	2W- and Y-olfactom., wind T, field trap	Attract. / Syn.of (LA, hand odor)	Bar-Zeev et al. (1977); Bernier et al. (2007); Eiras and Jepson (1991); Geier and Boeckh (1999); McMeniman et al. (2014)
		LA, AM, other	2W- and Y-olfactom.	Attract.	(Brown et al. 1951; Geier et al. 1999b; Mathew et al. 2013)
		OCT, other	2W-olfactom. + Field CDC, BG, FPT	Attract. / Syn.of (BG-lure)	Canyon and Hii (1997); Kawada et al. (2007); Mathew et al. (2013); Russell (2004)
		Hexanoic acid, FAs, aldehydes, other		Syn. (Hexanoic acid, FAs)	Owino et al. (2015); Peach et al. (2019b)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
			2W-olfactom. + Field BGS + GCEAD		
		Arm odor	2W-olfactom., wind T	Syn.of (arm odor)	Daykin et al. (1965); Dekker et al. (2005); Mayer and James (1969); Willis (1947)
		Human sweat, skin extracts, other	2W- and Y-olfactom., wind T	Attract./ Syn. (armpit sweat) / Syn.of (sweat extracts)	Brown et al. (1951); Dekker and Carde (2011); Eiras and Jepson (1991); Geier and Boeckh (1999); Geier et al. (1999b); Thompson and Brown (1955)
		Breath, other	2W-olfactom.	Syn.of (hand odor)	Daykin et al. (1965); DeGennaro et al. (2013)
		BG-lure	Field CDC, BGS	Syn.of (Linalool oxide) / No effect	Degener et al. (2019); Nyasembe et al. (2015); Rose et al. (2006)
	Ae. albopictus	-	Wind Tunnel + field CDC	Attract.	Klun et al. (2013); Saitoh et al. (2004)
		LA / Lurex3	2W-olfactom. + Field MMP	Attract. / Syn. (OCT + LA) / No effect	(Hoel et al. 2007); Kusakabe and Ikeshoji (1990); Xue et al. (2010)
		OCT	Field CDC, BGS	(Attract.) / No effect	Kawada et al. (2007); Shone et al. (2003)
		OCT, other	Field CDC, BGS, MMX	Attract. / Syn. (Hydroxycoumarins, OCT)	Andrianjafy et al. (2018); Cilek et al. (2012); Hoel et al. (2007); Xue et al. (2010)
		BG-lure	Field BGS, CDC, MKS	Syn.of (BG-lure)	Degener et al. (2019); Hoel et al. (2014b); Meeraus et al. (2008); Pombi et al. (2014); Sukumaran et al. (2016)
		Mouse odor, litter odor	Field BGS	Syn.of (mouse litter odor)	Le Goff et al. (2017)
	Ae. japonicus japonicus	LA, OCT, grass infusion, other	Field CDC	(Attract.) / Syn. (TrapTechLure)	Anderson et al. (2012); Balestrino et al. (2016)
	Ae. polynesiensis	OCT, BG-lure	Field CDC, BGS, EVS	Attract. / Syn. (OCT)	Hapairai et al. (2013); Russell (2004)
	Ae. taeniorynchus	OCT	Field CDC, PRO, CFG	Attract. / Syn. (OCT)	Kline et al. (1990a); Kline et al. (1991b); Kline (1999); Newhouse et al. (1966); Rueda et al. (2001); Takken and Kline (1989)
		OCT, LA, acetone, DMDS, 1-hexen-3-ol	Field MMX	Syn. (acetone + hexenol + OCT)	Kline et al. (2012)
	Ae. vexans	-	Ramp traps, Field CDC	Attract.	McIver and McElligott (1989); McPhatter and Gerry (2017)
		OCT	Field CDC, MMX, CFG	Attract. / Syn.of (OCT)	Becker et al. (1995); Burkett et al. (2001); Rueda et al. (2001)
	Ae. vigilax	OCT	Field EVS	Attract.	Essen et al. (1994); Kemme et al. (1993)
		Cyclopentanone	Field CDC	Attract. / Syn. (OCT)	Philippe-Janon et al. (2015)
	An. arabiensis	Human odor, other	Wind T., field CDC, OBETs	(Attract.) / Syn. (LA + AM)	Costantini et al. (1996); Dekker and Takken (1998); Hawaria et al. (2016); Omer (1979); Torr et al. (2008)
		MB5, Ifakara blend 1	3W-olfactom., field MMX	Syn. (MB5) / No effect	Lorenz et al. (2013); Mburu et al. (2017)
	An. aquasalis	OCT, human odors	Field CDC	(Attract.)	Hiwat et al. (2011); Rubio-Palis (1996)
	An. atroparvus	Rabbit/cattle blood odors	2W-olfactom.	Attract.	Laarman (1958)
	An. crucians	-	Field CDC	Attract.	Hoel et al. (2015); Newhouse et al. (1966)
		OCT, LA	Field CDC, MMpro	Attract. / Syn. (LA, OCT)	Kline et al. (2007); Kline et al. (1990a); Kline et al. (2012); Kline and Mann (1998); Xue et al. (2010)
	An. farauti	Foot odor, BG-lure, MB5	Suna traps	Attract.	van de Straat et al. (2019)
		Arm/hand odor	2W-olfactom.	Attract. / No effect	Price et al. (1979); Willis (1947)
	An. funestus	LA, human odor	Field OBEts, SSAM	Attract. / Syn. (LA)	Costantini et al. (1996); Murphy et al. (2001)
		MB5, BG-lure, Ifakara blend	Field BGS, MMX, HLC	(Attract.) / Syn. (MB5, BG-lure)	Batista et al. (2018); Mburu et al. (2017)
	An. gambiae	-	Wind T., field CDC. EAG	Attract.	Obenauer et al. (2013); Turner et al. (2011)
		Acetone, OCT	Wind T.	Syn. (Acetone)	Takken et al. (1997)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		Foot odors	Landing cage, field BGS, MMX	Attract. / Syn.of (foot odors)	Hawkes et al. (2012); Schmied et al. (2008); Smallegange et al. (2010); Webster et al. (2015)
		Foot odors, AM, LA, other	2W-olfactom. + Field MMX	Syn. (foot odors + AM)	Njiru et al. (2006); Spitzen et al. (2008)
		Foot odors, LA	2W-olfactom. + Field SSAM	Syn. (LA)	Dekker et al. (2002); Murphy et al. (2001)
		Human odor, other	2W-olfactom., Field MMX, OBETs	Attract.	Costantini et al. (1996); Healy and Copland (1995); Jawara et al. (2009); Lorenz et al. (2013); Pates et al. (2001)
		Limburger cheese	BGS in chamber	Syn.of (Limburger cheese)	Hoel et al. (2014b)
		MB5	Field MMX	Syn. (MB5)	Mburu et al. (2017)
		Foot odor, cow odor, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	An. melas	Calf odor	Ramp traps	(Attract.)	Gillies and Wilkes (1969); Gillies and Wilkes (1970)
	An. obscurus	Foot odor, cow odor, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	An. quadriannulatus	Human odor, other	Field CDC, OBETs	Attract. / Syn. (human odor)	Dekker and Takken (1998); Torr et al. (2008)
	An. quadrimaculatus	OCT	Field CDC	Attract. / Syn. (OCT)	Kline et al. (1991a); Kline et al. (1990b)
	An. stephensi	-	Field traps	No effect	Brouwer (1960)
		Acetone, OCT	Wind T.	Attract. / Syn. (OCT)	Takken et al. (1997)
		LA	2W-olfactom.	Attract. / Syn. (LA)	Omrani et al. (2012)
		BG-lure	Field MKS , BGS	Attract.	Sukumaran et al. (2016)
	C. decens	Foot odor, cow odor, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	C. nigripalpus	-	Field CDC	Attract.	Hoel et al. (2015); Newhouse et al. (1966)
		OCT, LA, other	Field CDC, MMpro	Attract. / Syn. (LA, OCT)	Hoel et al. (2007); Kline et al. (1990a); Kline et al. (1991b); (Kline et al. 2012); Xue et al. (2010)
		Rabbit odors, Chicken odors	Field traps	Attract.	Edman (1979)
	C. pipiens	-	Field CDC	Attract.	Saitoh et al. (2004)
		Hand odor	Wind T.	Attract.	Omer (1979)
		OCT	Field CDC	Attract.	Beavers et al. (1998); Becker et al. (1995)
		BG-lure, 2-undecanone	Field BGS, FPT	No effect	Rose et al. (2006)
	C. quinq.	-	Two-choice malariaSphere, Wind T., EAG-SSR, field BGS, CFG, CDC	Attract.	Cooperband and Cardé (2006); Jerry et al. (2017); Majeed et al. (2017); Oli et al. (2005); Reeves (1951); Turner et al. (2011)
		OCT	Field CDC, EVS	Attract.OCT	Cilek et al. (2012); Russell (2004); Vythilingam et al. (1992); Xue et al. (2010)
		cyclopentanone	2W-field exp. + Field CFG	Attract.	Tauxe et al. (2013)
		Foot odors, other	Wind T., field CDC, CFG	Attract. / Syn. (foot odors)	Lacey and Carde (2011); Mboera et al. (2000c)
		Human odor, chicken/mammal odors	Field EVS, CDC, OBETs. GC-EAD	Attract. / Syn. (nonanal)	Costantini et al. (1996); Mboera and Takken (1999); Syed and Leal (2009)
		Calf odor	Field traps	Attract.	Mboera and Takken (1999); Mullens and Gerry (1998); Reeves (1951)
		BG-lure	Field MKS, BGS	Attract.	Reeves (1953); Sukumaran et al. (2016)
	C. tarsalis	-	Wind T., field CDC, MMX	Attract.	Cooperband and Cardé (2006); McPhatter and Gerry (2017); Reeves (1953)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		Hand odor, mouse/chicken odors	2W-olfactom., field sticy traps	Attract. / Syn. (hand, mouse, chicken odors)	McIver (1968); Reeves (1951)
Cedrol	*An. gambiae*		2W-cages bioassays, BGS	Attract. (GF)	Lindh et al. (2015)
Cyclopentanone	*Ae. aegypti*	LA, butanone, AM, acetone	2W-olfactom.	Attract.	(Venkatesh and Sen 2017)
	Ae. albopictus	AM, Mix-5, BG-lure, LA, hexanoic acid, 3-methyl-1-butanol, cyclopentanone, 6M5H, OCT	4A-olfactom. + field BGS	Attract.	Xie et al. (2019)
	Ae. vigilax	CO_2	Field CDC	No effect	Philippe-Janon et al. (2015)
	C. quinq.	CO_2	4A-olfactom., 2W-field exp. + Field CFG	Attract. / No effect	Tauxe et al. (2013); Xie et al. (2019)
Decanal	*Ae. aegypti*	Hand odor, 6M5H, GA, octanal, nonanal	Y-T olfactom. Arm-in-cage, GC-EAD	No effect / Repellent	Logan et al. (2008); Logan et al. (2010)
	Ae. mcintoshi, Ae. ochraceus	Nonanal, octanal, heptanal	Field CDC, GC-EAD	Syn. (nonanal + heptanal + decanal)	Tchouassi et al. (2013)
	An. arabiensis	limonene, α-pinene, benzaldehyde, p-cymene	Y-T olfactom. Field BGS, GC-EAD	Syn. (limonene, α-pinene, benzaldehyde, p-cymene)	Wondwosen et al. (2016); Wondwosen et al. (2017)
	An. gambiae	linalool oxide, β-pinene, β-ocimene, hexanal, octanal, nonanal, limonene	2W-olfactom., field MMX	Syn. (heptanal + nonanal + octanal)	Jacob et al. (2018)
	C. quinq.	GA, 6M5H, Nonanal, octanal	2W-olfactom.	Syn. (nonanal + octanal)	Leal et al. (2017)
Dichloromethane	*Ae. aegypti, C. quinq., C. nigripalpus*	LA, DMDS, acetone	3-cages-2W-olfactom.	Syn. (LA)	Bernier et al. (2003)
	Ae. albopictus	LA, acetone, hand odor	Wind tunnel	Syn. (LA)	Hao et al. (2012)
Dimethyl disulfide	*Ae. aegypti*	CO_2, LA, acetone, dichlorométhane	Triple cage-2W-olfactom. + field CDC	Syn. (acetone, LA)	Allan et al. (2006); Bernier et al. (2007); Bernier et al. (2003); Silva et al. (2005)
	Ae. albopictus	CO_2, OCT, LA, AM, 6M5H, other	Y-T olfactom. Field MMX	Attract. / No effect	Cilek et al. (2012); Wang et al. (2006)
		3-methylindole, indole, 4-methylphenol, trimethylamine	Field ovitraps, sticky screen bioassays, EAG	No effect / Repellent	Trexler et al. (2003)
	Ae. japonicus japonicus	TrapTech Lure, CO_2, acetone, LA, FAs	Field CDC	Syn. (acetone, ethanol, LA)	Anderson et al. (2012)
	Ae. taeniorhynchus	CO_2, acetone, 1-hexen-3-ol, OCT, LA	Field MMX	Syn. (acetone + LA)	Kline et al. (2012)
	An. gambiae	AM, LA, TEA, skin microbiota odors	Triple cage-2W-olfactom.	Syn. (acetone + LA + TEA)	Verhulst et al. (2011b)
		Acetone, AM, LA, 7-octenoic acid, 1-dodecanol, 6M5H, GA, indole	2W-olfactom.	No effect	Qiu et al. (2011)
		DMDS, dimethyltrisulfide, nonane, 2,4-pentanedione	Ovip. Assays	Repellent (GF)	Schoelitsz et al. (2020)
4,5-Dimethylthiazole	*An. gambiae*	AM, LA, TEA, 29 other compounds	2W-olfactom., MMX	Syn. (AM + lactic acid + TEA)	Smallegange et al. (2012)
Dodecanoic acid	*Ae. aegypti*	(Z)-9-hexadecenoic acid, hexadecanoic acid, tetradecanoic acid	Bioassay ovipostion cages	Attract. (GF)	Ganesan et al. (2006); Sivakumar et al. (2011)
	Ae. albopictus	18 FAs	Y-olfactom.	Attract.	Seenivasagan et al. (2014)
	C. quinq.	hexadecanoic acid, tetradecanoic acid	Oviposition tests	Attract. (GF)	Sivakumar et al. (2011)
1-Dodecanol	*An. gambiae*		2W-olfactom., MMX	Attract. / No effect	Mweresa et al. (2016); Qiu et al. (2011)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		CO_2, AM, LA, 6M5H, DMDS, 2-pentadecanone, other			
Ethanol	*Ae. japonicus japonicus*	CO_2, LA, OCT, DMDS, FAs, TrapTech Lure, acetone	CDC	Syn. (DMDS + LA + acetone)	Anderson et al. (2012)
Ethyl acetate	*Ae. aegypti*	OCT, 6M5H, FAs	2W-olfactom.	Syn. (6M5H, acetic acid, ethyl alcohol)	Saratha and Mathew (2016)
Ethyl alcohol	*Ae. aegypti*	OCT, 6M5H, FAs	2W-olfactom.	Attract.	Saratha and Mathew (2016)
Ethyl butyrate	*Ae. albopictus*	LA, DMDS, 6M5H, hexanoic acid, OCT, AM	Y-olfactom., field traps	Attract.	Wang et al. (2006)
4-Ethylphenol	*Ae. albopictus*	Phenol, 4-methylphenol, indole, rat odor	Y-olfactom., BGS	Syn. (4-methylphenol)	Diaz-Santiz et al. (2020)
	C. quinq.	Indole, p-cresol, 3-ethylindole, grass infusion (Bermuda)	Bioassay cages	Syn. (blend)	Beehler et al. (1993); Beehler et al. (1994); Millar et al. (1992)
Formic acid	*Ae. aegypti*	OCT, 6M5H, acetic acid, other FA	2W-olfactom.	Attract.	Saratha and Mathew (2016)
Geranylacetone	*Ae. aegypti*	Hand odor, 6M5H, octanal, nonanal, decanal	Y-T olfactom. GC-EAD	Repellent	Logan et al. (2008); Logan et al. (2010)
((E)-6,10-Dimethyl-5,9-undecadien-2-one)	*An. gambiae*	Acetone, AM, LA, 6M5H, DMDS, octanal, nonanal, decanal	2W-olfactom. Arm-in-cage	Repellent	Logan et al. (2010); Qiu et al. (2011)
	C. pipiens pallens	OCT, benzaldehyde, p-cresol, TEA, FAs	Y-T olfactom. Field traps	Attract.	Tian et al. (2018)
	C. quinq.	6M5H, octanal, nonanal, decanal	2W-olfactom. Arm-in-cage	Repellent	Leal et al. (2017); Logan et al. (2010)
Geosmin	*Ae. aegypti*	Betroot peel	EAG, calcium imaging, field ovitraps	Attract. (GF)	Melo et al. (2020)
n-Heneicosane	*Ae. aegypti*		Y-olfactom., ovip. bioassays	Attract. (GF)	Baak-Baak et al. (2013); (Gonzalez et al. 2014); Seenivasagan et al. (2009); Suman (2019)
		4-methylphenol, 3-methylindole (skatole), phenol	Ovitraps	Attract. (GF)	Baak-Baak et al. (2013)
	Ae. albopictus	Other oviposition attractant	Ovip. Bioassays, EAG	Attract. (GF)	Gonzalez et al. (2014); Suman (2019)
Heptanal	*Ae. mcintoshi, Ae. ochraceus*	Nonanal, octanal, decanal	Field CDC, GC-EAD	Syn. (nonanal + octanal + decanal)	Tchouassi et al. (2013)
	An. gambiae	Plant odor, β-pinene, limonene, linalool oxide, nonanal, decanal, other	2W-olfactom., field MMX, GC-EAD	Syn. (nonanal + octanal + decanal)	Jacob et al. (2018); Nyasembe et al. (2012)
Heptanoic acid	*Ae. aegypti*	OCT, 6M5H, acetic acid, other FAs	2W-olfactom.	No effect	Saratha and Mathew (2016)
	Ae. albopictus	TEA, butanoic acid, propanoic acid, hexanoic acid, octanoic acid + 12 other FAs	Y-T olfactom.	No effect	Seenivasagan et al. (2014)
	An. gambiae	CO_2, AM, LA, TEA, FAs	2W-olfactom. + Field MMX	No effect / Repellent	Jawara et al. (2011); Smallegange et al. (2009)
	C. pipiens pallens	OCT, benzaldehyde, p-cresol, TEA, FAs	Y-T olfactom. Field traps	No effect	Tian et al. (2018)
3-Heptanol	*An. gambiae*	AM, LA, TEA, other	2W-olfactom., MMX	Attract.	Smallegange et al. (2012)
Hexanal	*Ae. aegypti*	CO_2, AM, OCT, FAs, other	2W-olfactom.	No effect	Mathew et al. (2013)
	An. gambiae	Plant odor, β-pinene, limonene, linalool oxide, nonanal, decanal, other	2W-olfactom., field MMX, GC-EAD	Syn. (linalool oxide)	Jacob et al. (2018); Nyasembe et al. (2012)
	C. pipiens pallens	OCT, FAs, terpenes, other	Y-T olfactom. Field traps	Attract.	Tian et al. (2018); Yu et al. (2015)
Hexanol	*C. pipiens pallens*	18 COVs, terpenes, aldehydes…	Y-T olfactom.	Attract. / Syn. (blend 6 compounds)	Yu et al. (2015)
Hexanoic acid	*Ae. aegypti*	CO_2, 3-methylbutyric acid, propionic acid, nonanal, octanal, foot odor	Field BGS + GC-EAD	Attract.	Carlson et al. (1973); Owino et al. (2015)
		CO_2, AM, OCT, FAs, other	2W-olfactom.	No effect	Mathew et al. (2013); Peach et al. (2019b)
		Hand odor, LA, AM	Y-T olfactom.	Syn. (LA)	Williams et al. (2006b)
		Hand odor, acetone, BG lure	Y-T olfactom., field BGS	Syn. (BG-lure)	Williams et al. (2006a)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		Linalool oxide	Fiel BGS	Attract.	Omondi et al. (2019)
	Ae. albopictus	Mix-5, BG-lure, AM, LA, OCT, DMDS, FAs, 6M5H	Y-T and 4W- olfactom. Field traps	Attract.	Seenivasagan et al. (2014); Wang et al. (2006); Xie et al. (2019)
	An. gambiae	CO_2, LA, human odor, FAs	Field trap	No effect	Murphy et al. (2001)
1-Hexen-3-ol	*Ae. aegypti*	CO_2, AM, LA, FAs, OCT, other	2W-olfactom.	No effect	Mathew et al. (2013)
	Ae. taeniorhynchus, An. crucians	CO_2, Acetone, OCT, LA, DMDS	MM experim. traps	Syn. (acetone + otcenol)	Kline et al. (2012)
4-Hydroxycoumarin	*Ae. albopictus*	CO_2, OCT, other hydroxycoumarins	Cage traps, BGS	Attract. / Syn. (OCT)	Andrianjafy et al. (2018)
	A. sp	CO_2, OCT	CDC LT	Attract. / Syn. (OCT)	Andrianjafy et al. (2020)
Indole	*Ae. albopictus*	Phenol, 4-methylphenol, 4-ethylphenol, rat odor	Y-olfactom., BGS	Syn. (4-methylphenol + 4-ethylphenol)	Diaz-Santiz et al. (2020)
		DMDS, 3-methylindole, 4-methylphenol, trimethylamine	Field ovitraps, sticky screen bioassays, EAG	No effect / Repellent	Trexler et al. (2003)
	An. gambiae	6M5H, GA, human sweat extracts	2W-olfactom., EAG	Attract. / No effect	Meijerink et al. (2000); Qiu et al. (2011)
	C. quinq.	Phenol, 4-methylphenol, 4-ethylphenol, 3-methylindole (skatole), grass infusion (Bermuda)	Bioassays cages	Attract. (3-methylindole)	Beehler et al. (1993); Beehler et al. (1994); Millar et al. (1992)
Isovaleric acid	*Ae. albopictus*	OCT	Cage with bottle traps	Attract.	Andrianjafy et al. (2017)
	C. quinq.	OCT	Cage with bottle traps	Attract.	Andrianjafy et al. (2017)
Lactic acid	*Ae. aegypti*	CO_2	2W-olfactom. Field traps	Syn. (CO_2)	Acree et al. (1968); Kusakabe and Ikeshoji (1990)
		CO_2, acetone, DMDS	Triple cage-2W-olfactom. + Field CDC, CFG	Syn. (acetone, DMDS)	Bernier et al. (2007); Bernier et al. (2003); Silva et al. (2005)
		CO_2, AM + other compounds	Y- and 2W-olfactom. MMX traps	Attract. / Syn. (AM) / No effect	Brown et al. (1951); Geier et al. (1999a); Geier et al. (2002); Mathew et al. (2013); Menger et al. (2015); Menger et al. (2014a); Williams et al. (2006b)
		CO_2, OCT	Field FP traps, HLC	Repellent	Canyon and Hii (1997)
		AM, acetone, butanone, cyclopentanone	2W-olfactom.	Syn. (Acetone + butanone)	Venkatesh and Sen (2017)
		FAs	Y-olfactom.	Attract. / Syn. (CO_2) / Syn.of (propanoic acid, valeric acid)	Allan et al. (2006); Bosch et al. (2000); Carlson et al. (1973); Geier et al. (2002); Müller (1968)
		Hand odor	Y- and 2W-olfactom. Field traps	Attract. / Syn. (CO_2, AM, caproic acid) / Syn.of (Hand odor)	Eiras and Jepson (1991); Geier and Boeckh (1999); Geier et al. (1996); McMeniman et al. (2014); Williams et al. (2006b)
		CO_2, sweat samples	2W-olfactom. + wind T.	Syn. (CO_2) / No effect	Brown et al. (1951); Eiras and Jepson (1994); Eiras and Jepson (1991)
		CO_2, skin extracts	2W-olfactom. + wind T. Field traps	Attract. / Syn. (CO_2, AM)No effect	Geier and Boeckh (1999); Geier et al. (1999a); Geier et al. (1996); McMeniman et al. (2014); Smith et al. (1970); Steib et al. (2001)
		CO_2, forearm odor	2W-olfactom.	Attract.	Bar-Zeev et al. (1977)
		Bovine and avian blood, FAs	Triple cage-2W-olfactom.	Attract.	Allan et al. (2006)
		OCT, Mango odors	3cages 2W-olfactom. + field BGS	Syn. (Mango odors + OCT)	Scott-Fiorenzano et al. (2017)
	Ae. albopictus	CO_2, OCT	Field MMP traps	Syn. (CO_2 + OCT)	Hoel et al. (2007)
		AM, OCT, 6M5H + other	Y- and 4W-olfactom. Field traps	Attract. / No effect	Wang et al. (2006); Xie et al. (2019)
		Hand odor, acetone, dichloromethane	Wind T.		Hao et al. (2012)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
				Syn. (acetone, dichloromethane)	
		2-methyl-3-pentanol, OCT	Y-olfactom., EAG	Attract.	Guha et al. (2014)
		OCT, Mango odors	3cages 2W-olfactom. + field BGS	No effect	Scott-Fiorenzano et al. (2017)
	An. arabiensis	CO_2, AM, foot odors, cow urine	Field odor-baited sticky trap	Syn. (CO_2, AM)	Hawaria et al. (2016)
	An. coluzzii	AM, TEA, 3-methyl-1-butanol, other	2W-olfactom. + wind T.	Syn. (AM, TEA)	van Loon et al. (2015)
	An. gambiae	AM, TEA, 3-methyl-1-butanol	2W-olfactom. + wind T. Field MMX	Syn. (CO_2, AM, TEA, 3-methyl-1-butanol)	Menger et al. (2015); Menger et al. (2014a); Menger et al. (2014b); Verhulst et al. (2011a)
		AM, TEA + other	2W-olfactom. + Field MMX	Syn. (AM, TEA)	Jawara et al. (2011); Smallegange et al. (2012); Smallegange et al. (2009); Verhulst et al. (2010a); Verhulst et al. (2011a)
		AM, FAs	2W-olfactom. + Field MMX	Syn. (AM, FAs)	Jawara et al. (2011); Qiu et al. (2011); Smallegange et al. (2009); Smallegange et al. (2005)
		AM, sweat odors	2W-olfactom. + wind T.	No effect	Braks et al. (2001); Healy and Copland (2000)
		CO_2, human odors	Y- and 2W-olfactom. Field traps	Syn. (CO_2, skin odors)	Braks et al. (2001); Dekker et al. (2002); Healy and Copland (2000); Murphy et al. (2001); Smallegange et al. (2002)
		CO_2, AM, foot odors	2W-olfactom.	Syn. (CO_2 + AM)	Spitzen et al. (2008)
		Goat odor	Trapping huts	Attract. / Syn. (Goat odor)	Kemibala et al. (2020)
	Ae. japonicus japonicus	CO_2, acetone, DMDS, other	Field CDC	Syn. (CO_2, OCT)	(Anderson et al. 2012)
	An. stephensi	CO_2	2W-olfactom.	Syn. (CO_2)	Omrani et al. (2012)
	Ae. taeniorhynchus	CO_2, OCT, acetone, other compounds	Field CDC	Syn. (CO_2, acetone)	Kline et al. (1990a); Kline et al. (2012)
	C. nigripalpus	CO_2, OCT, other compounds	2W and 4W-olfactom. Field traps	Syn. (CO_2 + OCT)	Allan et al. (2006); Hoel et al. (2007); Kline et al. (1990a); Kline et al. (2012)
	C. pipiens	CO_2, ammonium hydroxyde, molasse	Trapping boxes	Syn. (CO_2)	El-Sisi et al. (2019)
	C. quinq.	AM, OCT, FAs, other	Triple cage-2W and 4W-olfactom.	Attract.	Allan et al. (2006); Xie et al. (2019)
Lilac aldehyde	*Ae. species*	Platanthera odors, nonanal	Y-maze olfactom., GC-EAD, calcum imaging	Attract.	Lahondere et al. (2020)
Limonene	*An. arabiensis*	6M5H, nonanal, other	Field CDC. GC-EAD	No effect	Jaleta et al. (2016)
	An. gambiae	Plant odors, terpenes, other	2W-olfactom. + field CDC, MMX. GC-EAD	Attract. / Syn. (mammal/plant odors)	Jacob et al. (2018); Nyasembe et al. (2012)
	C. pipiens pallens	Terpenes, aldehydes, other	Y-olfactom.	(Attract.)	Yu et al. (2015)
Linalool oxide	*Ae. aegypti*	hexanoic acid	Fiel BGS	Attract.	Omondi et al. (2019)
	An. gambiae	Plant odor, nonanal, hexanal, β-pinene, β-ocimene, limonene, other	2W-olfactom., GCE-AD, MMX	Attract. / Syn. (β-pinene + β-ocimene)	Jacob et al. (2018); Nyasembe et al. (2012); Nyasembe and Torto (2014)
		CO_2, BG lure, Honad lure	CDC	Syn. (CO_2)	Nyasembe et al. (2015)
	C. pipiens pallens	Nonanal, aldehydes, terpenes	Y-olfactom.	Attract.	Yu et al. (2015)
Lysine	*Ae. aegypti*	Alanine	Bioassays cages	Attract.	Brown and Carmichael (1961)
3-Methylbutanal	*An. gambiae*	AM, LA, FAs, TEA	2W-olfactom., MMX	Syn. (blend)	Verhulst et al. (2009); Verhulst et al. (2011a)
3-Methyl-1-butanol	*Ae. aegypti*	CO_2, AM, LA, TEA, butan-1-amine	Flight chamber	Syn. (CO_2 + AM + LA + TEA + butan-1-amine)	Menger et al. (2014b)
	Ae. albopictus	Mix-5, BG-lure, AM LA, hexanoic acid, other	4A-olfactom. + field BGS	Attract.	Xie et al. (2019)
		dodecenol, 2-methyl-1-butanol, skin bacteria odors	Olfactom.		Michalet et al. (2019)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
				Syn. (dodecenol + 2-methyl-1-butanol)	
	An. coluzzii	AM, LA, TEA, butan-1-amine, 3-methyl-butanoic acid, 3-methyl-butanoic acid, 3-methylbutanal	2W-olfactom.	Syn. (CO_2 + AM + LA + TEA)	van Loon et al. (2015)
	An. gambiae	CO_2	Field CDC	No effect	Zohdy et al. (2015)
		AM, LA, TEA, butan-1-amine	2W-olfactom. + Field MMX	Syn. (CO_2 + AM + LA + TEA + butan-1-amine)	Menger et al. (2015); Menger et al. (2014a); Menger et al. (2014b); Mukabana et al. (2012b); Verhulst et al. (2009); Verhulst et al. (2011a)
3-Methylbutanoic acid	*Ae. aegypti*	Tansy flowers odor, synthetic blend	2W-bioassays	Syn. (synth. Blend)	Peach et al. (2019b)
	An. gambiae	AM, LA, FAs, TEA, other	2W-olfactom., MMX	Syn. (blend)Repellent	Smallegange et al. (2009); Verhulst et al. (2009); Verhulst et al. (2011a)
6-Methyl-5-hepten-2-one	*Ae. aegypti*	GA, nonanal, octanal + other compounds	Y-olfactom., arm in cage, GC-EAD	Repellent	Logan et al. (2008); Logan et al. (2010)
(Sulcatone)		Hand odor + other compounds	2W-olfactom. + GC-SSR	Attract.	Bernier et al. (2002); McBride et al. (2014)
		OCT, FAs, other compounds	2W-olfactom.	Attract. / Syn. (acetic acid, ethyl acetate, ethyl alcohol)	Saratha and Mathew (2016)
	Ae. albopictus	LA, AM, hexanoic acid + other compounds	Y- and 4A-olfactom. + field BGS	Attract.	Wang et al. (2020); Xie et al. (2019)
	An. arabiensis	Limonene, nonanal + other compounds	2W-olfactom. + GC-EAD + field BGS	Syn. (decanal, nonanal + terpenes) / No effect	Jaleta et al. (2016); Wondwosen et al. (2016)
	An. gambiae	GA + other compounds	2W-olfactom., arm in cage	No effect / Repellent	Logan et al. (2010); Qiu et al. (2011)
	C. quinq.	GA, Octanal, Nonanal, Decanal	2W-olfactom.	No effect / Repellent	Leal et al. (2017)
		LA, AM, hexanoic acid + other compounds	4A-olfactom. + field BGS	Attract.	Xie et al. (2019)
2-Methyl-3-pentanol	*Ae. albopictus*	LA, OCT	Y-olfactom., EAG	Attract.	Guha et al. (2014)
4-Methylphenol (p-Cresol)	*Ae. aegypti*	n-heneicosane, 3-methylindole (skatole), phenol	Ovitraps	Attract. (GF)	Baak-Baak et al. (2013)
	Ae. albopictus	Phenol, ethylphenol, indole, rat odor	Y-olfactom., BGS	Syn. (ethylphenol)	Diaz-Santiz et al. (2020)
		DMDS, 3-methylindole, indole, trimethylamine	Field ovitraps, sticky screen bioassays, EAG	No effect / Repellent	Trexler et al. (2003)
	Ae. triseriatus	Betula papyrifera extracts	Bioassay cages, ovip. traps	Attract. (GF)	Bentley et al. (1979)
	An. arabiensis, An. quadriannulatus	Human odor, ox odout, acetone, OCT, 3-n-propylphenol	OBET, E-nets, CDC	Syn. (acetone, 1-octen-3-ol, and 3-n-propylphenol)	Torr et al. (2008)
	C. pipiens pallens	OCT, GA, FAs	Y-olfactom., baited traps	(Attract.)	Tian et al. (2018)
	C. quinq.	4-ethyphenol, indole, 3-ethylindole, grass infusion (Bermuda)	Bioassay cages	Syn. (blend)	Beehler et al. (1993); Beehler et al. (1994); Millar et al. (1992)
2-Methylpropanal	*An. gambiae*	AM, LA, TEA, 29 other compounds	2W-olfactom., MMX	Syn. (AM + lactic acid + TEA)	Smallegange et al. (2012)
Methyl sulfide	*Ae. aegypti*	Bovine/avian blood, LA, DMDS, other	Triple-cage 2W-olfactom.	Attract.	Allan et al. (2006)
Nonanal	*Ae. aegypti*	CO_2, human odor, octanal, FAs	Field BGS, GC-EAD	Syn. (octanal)	Owino et al. (2015)
		Hand odor, 6M5H, GA, octanal, decanal		No effect / Repellent	Logan et al. (2008); Logan et al. (2010)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
			Y-T olfactom. Arm-in-cage, GC-EAD		
	Ae. mcintoshi, Ae. ochraceus	Heptanal, octanal, decanal	Field CDC, GC-EAD	Syn. (Heptanal + octanal + decanal)	Tchouassi et al. (2013)
	An. arabiensis	6M5H, limonene, other	Field CDC, GC-EAD	No effect	Jaleta et al. (2016)
		limonene, α-pinene, benzaldehyde, p-cymene	Y-T olfactom. Field BGS, GC-EAD	Syn. (limonene, α-pinene, benzaldehyde, p-cymene)	Wondwosen et al. (2016); Wondwosen et al. (2017)
	An. gambiae	6M5H, GA, octanal, decanal	Arm-in-cage	Repellent	Logan et al. (2010)
		linalool oxide, β-pinene, β-ocimene, hexanal, octanal, decanal, limonene	2W-olfactom., field MMX	Syn. (Heptanal + octanal + decanal)	Jacob et al. (2018)
	C. quinq.	Human odor, CO_2, 6M5H, GA, octanal, decanal, other	2W and Y-T olfactom., field EVS, arm-in--cage, EAG	Attract.	Leal et al. (2017); Logan et al. (2010); Puri et al. (2006); Syed and Leal (2009)
	C. pipiens pallens	18 COVs, terpenes, aldehydes…	Y-T olfactom.	Attract.	Yu et al. (2015)
Nonanoic acid	*Ae. aegypti*	6M5H, OCT + FAs	2W-olfactom.	Attract.	Saratha and Mathew (2016)
		Tetradecanoic acid, tetradecanoic methyl ester	Behav. bioassays	Attract. (GF)	Ponnusamy et al. (2008)
	An. gambiae	CO_2, AM, LA, FAs, other	2W-olfactom. + Field MMX	No effect	Bernier et al. (2003); Smallegange et al. (2009)
(E)-2-Nonenal	*C. pipiens*	Milkweed flower extracts, benzaldehyde, phenylacetaldehyde	2W-flight olfactom.	Syn. (benzaldehyde + phenylacetaldehyde)	Otienoburu et al. (2012)
β-Ocimene	*An. gambiae*	(E)-linalool oxide, β-pinene, nonanal, hexanal, octanal, decanal, limonene	2W-olfactom., MMX	Syn. ((E)-linalool oxide + β-pinene)	Jacob et al. (2018)
Octanal	*Ae. aegypti*	CO_2, human odor, nonanal, FAs	Field BGS, GC-EAD	Attract. / Syn. (nonanal)	Owino et al. (2015)
		Hand odor, 6M5H, GA, nonanal, decanal	Y-T olfactom. Arm-in-cage, GC-EAD	No effect / Repellent	Logan et al. (2008); Logan et al. (2010)
	Ae. mcintoshi, Ae. ochraceus	Nonanal, heptanal, decanal	Field CDC, GC-EAD	Syn. (Nonanal + heptanal + decanal)	Tchouassi et al. (2013)
	An. gambiae	6M5H, GA, nonanal, decanal	Arm-in-cage	Repellent	Logan et al. (2010)
		linalool oxide, β-pinene, β-ocimene, hexanal, octanal, decanal, limonene	2W-olfactom., field MMX	Syn. (Heptanal + nonanal + decanal)	Jacob et al. (2018)
		AM, LA, TEA, 29 other compounds	2W-olfactom., field MMX	Syn. (AM + LA + TEA)	Smallegange et al. (2012)
	C. quinq.	GA, 6M5H, Nonanal, Decanal	2W-olfactom., arm-in-cage	Nonanal + decanal	Leal et al. (2017); Logan et al. (2010)
Octanoic acid	*Ae. aegypti*	CO_2, AM, LA, OCT, FAs, terpenes, aldehydes		Repellent	Mathew et al. (2013)
	Ae. albopictus	TEA, butanoic acid, propanoic acid, hexanoic acid, heptanoic acid + 12 other carboxylic acids	Y-olfactom.	Attract.	Seenivasagan et al. (2014)
	An. gambiae	CO_2, AM, LA, FAs, other	2W-olfactom. + Field MMX	Syn. (LA + AM)	Jawara et al. (2011); Smallegange et al. (2009)
	C. pipiens pallens	OCT, benzaldehyde, p-cresol, GA, propionic acid, hexanal, TEA, heptanoic acid	Y-olfactom. + field	Attract.	Tian et al. (2018)
7-Octenoic acid	*An. gambiae*	CO_2, LA, AM, 6M5H, DMDS, other	2W-olfactom., wind T, OBET	Attract. / Syn. (AM + LA)	Costantini et al. (2001); Qiu et al. (2011)
1-Octen-3-ol	*Ae. aegypti*	CO_2	Field CDC, EVS, BG	Syn. (CO_2) / No effect	Hapairai et al. (2013); Kawada et al. (2007); Russell (2004)
		CO_2, LA + other compounds	Y- and 2W-olfactom. + field FP	Attract. / Repellent	Canyon and Hii (1997); Cook et al. (2011a); Mathew et al. (2013)
		Hand, cattle, or chicken odors	Landing bioass. + SSR	Syn. (Hand or cattle odors)	Majeed et al. (2016)
		Mushroom odors	Y-olfactom.	Attract.	Chaiphongpachara et al. (2019)
		Mango odors		Syn. (Mango odors)	Scott-Fiorenzano et al. (2017)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
			3cages 2W-olfactom. + field BGS		
		BG-lure	Field CDC's AOG	No effect	Liu et al. (2019)
		6M5H + FAs	2W-olfactom.	Attract.	Saratha and Mathew (2016)
	Ae. albopictus	CO_2	Field CDC F-P + MMX pro	Attract. / Syn. (CO_2) / No effect	Kawada et al. (2007); Qualls and Mullen (2007); Shone et al. (2003); Vythilingam et al. (1992)
		CO_2 + LA	Field MMX pro	Syn. (CO_2, LA)	Hoel et al. (2007); Xue et al. (2010)
		CO_2 + other compounds	Lab cages + field MMX	Attract. / Syn. (CO_2 or 3, 4 and 6-hydroxycoumarins)	Andrianjafy et al. (2017); Andrianjafy et al. (2018); Cilek et al. (2012)
		LA + other compounds	2W+4A olfactom. + field BGS MMX + EAG	Attract.	Guha et al. (2014); Li et al. (2010); Scott-Fiorenzano et al. (2017); Wang et al. (2006); Xie et al. (2019)
		BG-lure	Field BGS	Syn. (CO_2, BG-lure) / No effect	Roiz et al. (2016); Unlu et al. (2016)
	Ae. japonicus japonicus	TrapTech Lure, CO_2, acetone, LA, FAs	Field CDC	Attract.	Anderson et al. (2012)
	Ae. polynesiensis	CO_2, human odor, BG-lure	Field BGS, BGM, HBC	Syn. (CO_2)	Hapairai et al. (2013)
	Ae. taeniorhynchus	CO_2	Field CDC	Attract. / Syn. (CO_2)	Kline et al. (1991b); Kline (1999); Takken and Kline (1989)
		CO_2, LA + other compounds	Field CDC	Syn. (CO_2)	Kline et al. (1990a)
	Ae. vexans	CO_2	Field CDC	Syn. (CO_2)	Burkett et al. (2001); (Rueda et al. 2001)
		CO_2, hamster odor	Field CDC	No effect	Becker et al. (1995)
	Ae. vigilax	CO_2	Field EVS, CDC	Attract.	Essen et al. (1994); Kemme et al. (1993)
	An. aquasalis, An. albimanus	CO_2	Field CDC	No effect	Rubio-Palis (1996)
	An. crucians	CO_2	Field CDC, MMX, Coleman MD	Syn. (CO_2)	Kline et al. (2007); Kline et al. (1991a); Kline and Mann (1998)
		CO_2, LA + other compounds	Field CDC, MMX	Syn. (CO_2 or acetone+ hexenol)	Kline et al. (1990a); Kline et al. (2012)
	A. darlingi		Field MM LP, CDC, HLC	Attract.	Vezenegho et al. (2014)
	An. gambiae	CO_2, acetone	Wind T.	Syn. (CO_2)	Takken et al. (1997)
		CO_2, AM, foot odors	Semi-field MMX	No effect	Njiru et al. (2006)
	An. stephensi	CO_2, acetone	Wind T.	Syn. (CO_2)	McBride et al. (2014); Takken et al. (1997)
	A. species	CO_2	Field EVS	Syn. (CO_2) / No effect	Burkett et al. (2001); Cooper et al. (2004); Torr et al. (2008)
	C. pipiens	CO_2	Field SCFG, CDC, MM	No effect	Beavers et al. (1998); Becker et al. (1995)
		benzaldehyde, p-cresol, GA, propionic acid, TEA, hexanal, octanoic acid, heptanoic acid	Y-olfactom. + field	Attract. / Syn. (benzaldehyde, hexanal, TEA, propionic acid)	Tian et al. (2018)
	C. quinq.	CO_2	2W+4A olfactom., field MMX	Attract. / Syn. (CO_2)	Andrianjafy et al. (2017); Cilek et al. (2012); Vythilingam et al. (1992)
		CO_2 + other compounds	Fiel CFG, BG, CDC	No effect / Repellent	Cook et al. (2011b); Jerry et al. (2017); Russell (2004); Xue et al. (2010)
		Hand, cattle, or chicken odors	Landing bioass. + SSR	Syn. (hand or cattle odors)	Majeed et al. (2016)
		CO_2, foot odors, acetone	Fiel CFG + CDC	No effect	Mboera et al. (2000c)
	C. salinarius	CO_2	CDC, MMX, coleman	Attract.	Kline et al. (2007); Kline et al. (1991a); Kline and Mann (1998)
Oxocarboxylic acids	*An. gambiae*		Wind Tunnel	Attract.	Healy et al. (2002)
2-Oxopentanoic acid	*An. gambiae*	LA, FAs, human sweat	Wind Tunnel	Attract.	Healy and Copland (2000); Healy et al. (2002)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
2-Pentadecanone		CO_2, AM, LA, TEA, other	3-cages-2W-olfactom., MMX		Mweresa et al. (2016); Verhulst et al. (2010a)
Pentanoic acid	*An. gambiae*	AM, LA, TEA, FAs	2W-olfactom., MMX	Syn. (ammnonia + LA)	Smallegange et al. (2009)
Phenyl acetaldehyde	*C. pipiens*	Milkweed flower extracts, benzaldehyde, (E)-2-nonenal	2W-olfactom.	Syn. (benzaldehyde +(E)-2-nonenal)	Otienoburu et al. (2012)
	C. tarsalis		Suger bait stations	Syn. (Sugar baits)	Lothrop et al. (2012)
β-Pinene	*An. gambiae*	Linalool oxide, β-ocimene, nonanal, hexanal, octanal, decanal, limonene	2W-olfactom., GCE-AD, MMX	Syn. (linalool oxide + β-ocimene)	Jacob et al. (2018); Nyasembe et al. (2012); Nyasembe and Torto (2014)
	C. pipiens pallens	18 compounds	Y-olfactom.	Attract.	Yu et al. (2015)
Propionic acid	*Ae. aegypti*	CO_2, LA, acetic acid, hexanoic acid, FA	Y-olfactom. + field BGS, GC-EAD	Attract. / Syn. (LA, 3-methylbutyric acid)	Bosch et al. (2000); Carlson et al. (1973); Owino et al. (2015)
		6M5H, OCT + FAs	2W-olfactom.	Repellent	Saratha and Mathew (2016)
	Ae. albopictus	TEA, butanoic acid, octanoic acid, hexanoic acid, heptanoic acid + 12 other carboxylic acids	Y-olfactom.	Attract.	Seenivasagan et al. (2014)
	Ae. japonicus japonicus	TrapTech Lure, CO_2, acetone, OCT, LA, FAs	Field CDC	Attract. / No effect	Anderson et al. (2012)
	An. gambiae	CO_2, AM, LA, FAs, other	2W-olfactom. + Field MMX	Syn. (LA + AM)	Jawara et al. (2011); Smallegange et al. (2009)
	C. pipiens pallens	OCT, benzaldehyde, p-cresol, GA, octanoic acid, hexanal, TEA, heptanoic acid	Y-olfactom. + field	Attract.	Tian et al. (2018)
Propyloctadecanoate	*Ae. aegypti, Ae. albopictus*	FA	Oviposition bioassays, Flight behav., EAG	Attract. (GF)	Seenivasagan et al. (2012); Sharma et al. (2008); Sharma et al. (2009)
Skatole (3-Methylindole)	*Ae. aegypti*	n-heneicosane, phenol, 4-methylphenol)	Ovitraps	Attract. (GF)	Baak-Baak et al. (2013)
	Ae. albopictus	DMDS, 4-methylphenol, indole, trimethylamine	Field ovitraps, sticky screen bioassays, EAG	No effect / Repellent	Trexler et al. (2003)
	C. quinq.	Phenol, 4-methylphenol, 4-ethylphenol, grass infusion (Bermuda)	Bioassays cages	Syn. (indole)	Beehler et al. (1993); Beehler et al. (1994); Millar et al. (1992)
		6-acetoxy-5-hexadecanolide (plant derived)	2W-olfactom., ovitraps, EAG	Syn. (6-acetoxy-5--hexadecanolid) / No effect	Blackwell et al. (1993); Mboera et al. (2000a); Olagbemiro et al. (2004); Paiva et al. (2019)
Stearic acid	*Ae. aegypti, Ae. albopictus*		UV LED trapping device	Attract.	Tseng et al. (2019)
Tetradecanoic acid	*Ae. aegypti*	CO_2, AM, LA, OCT, FAs, terpenes, aldehydes		Attract. / Syn. (CO_2, LA, AM, OCT)	Mathew et al. (2013)
		Nonanoic acid, tetradecanoic methyl ester	Behav. bioassays	Attract. (GF)	Ponnusamy et al. (2008)
		hexadecanoic acid, dodecanoic acid	Oviposition tests	Attract. (GF)	Sivakumar et al. (2011)
	Ae. albopictus	butanoic acid, propanoic acid, hexanoic acid, heptanoic acid, octanoic acid + 12 other carboxylic acids	Y-olfactom.	Attract.	Seenivasagan et al. (2014)
	An. coluzzii	LA, AM, butan-1-amine, 3-methyl-1-butanol, 3-methyl-butanoic acid, 3-methyl-butanoic acid, 3-methylbutanal	2W-olfactom.	Syn. (LA + AM)	van Loon et al. (2015)
	An. gambiae	CO_2, AM, LA, FAs, other	2W-olfactom. + Field MMX	Attract. / Syn. (LA + AM)	Jawara et al. (2011); Smallegange et al. (2012); Smallegange et al. (2009)
		CO_2, AM, LA, 3-methyl-1-butanol, butan-1-amine	2W-olfactom. + Field MMX	Syn. (CO_2 + AM + LA + 3-methyl-1-butanol + butan-1-amine)	Menger et al. (2015); Menger et al. (2014a); Menger et al. (2014b); Mukabana et al. (2012b); Verhulst et al. (2009); Verhulst et al. (2011a)
	C. pipiens pallens	OCT, benzaldehyde, p-cresol, GA, propionic acid, hexanal, octanoic acid, heptanoic acid	Y-olfactom. + field	Attract.	Tian et al. (2018)18
	C. quinq.	hexadecanoic acid, dodecanoic acid	Oviposition tests	Attract. (GF)	Sivakumar et al. (2011)

Table 1 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
Valeric acid	*Ae. aegypti*	LA, FAs	Y-olfactom.	Attract. / Syn. (LA)	Bosch et al. (2000); Carlson et al. (1973)
	Ae. japonicus japonicus	CO_2, OCT, LA, DMDS, TrapTech Lure, grass infusion, propionic acid, butyric acid	CDC	Syn. (OCT+propionic+butyric acid)	Anderson et al. (2012)

Abbreviations used (Mosquito species): quinq (quinquefasciatus)

Abbreviations used (Compounds): AM (ammonia), CO_2 (Carbon dioxide), DMDS (Dimethyl disulfide), LA (lactic acid), FAs (fatty acids), GA (geranylacetone), 6M5H (6-methyl-5-hepten-2-one), 1-octen-3-ol (OCT), TEA (tetradecanoic acid)

Abbreviations used (Method): 2W-olfactom. (2-way olfactometer), 4A-olfactom. (4-arms olfactometer), Y-olfactom. (Y-olfactometer), Wind t. (wind tunnel), EAG (electroantennography), GC-EAD (gas chromatography/ electroantennodetection), SSR (single sensillum recording). Trap types : BG or BGS (Biogents trap or BG Sentinel trap), MMX or MMLP (Mosquito Magnet-X trap, MM Liberty Plus trap), CDC (Centers for Disease Control trap or CDC miniature light trap), CFG (CounterFlow Geometry trap), EVS (Encephalitis Vector Survey trap), FPT (Fay-Prince Trap), HDT (Host Decoy Trap), HLC (Human Landing Collection method), MKS (Mosquito Killing System), Obet (Odour-Baited Entry Trap), SSAM (Solid State Army Miniature light trap).

Abbreviations used (Effect): GF (Gravid females).

mosquito behaviour, and effects of combinations of compounds (including synergy). Data are synthesized in Tables 1 to 3.

Most Common Effective Attractants

"Mosquito attractants" in this review are divided into three main categories: (i) single volatile compounds that have been proved to be attractive in the absence of any other odorant source or in combination with other compounds; (ii) host or plant natural odors or odor extracts; (iii) blends of volatile compounds, such as synthetic blends and commercial lures. All the individual compounds, natural odors from living organisms, or synthetic blends that are attractive to adult mosquitoes are presented in Tables 1, 2, and 3, respectively. A total of 77 compounds, 17 organism odors, and 11 synthetic blends have been observed to attract mosquitoes.

In this section, we present the most common effective attractants (see Fig. 1). These are volatile compounds or odors already well known for their efficacy in trapping adult mosquitoes, and they have been proved attractive in more than 70% of the studies that examined these compounds. Compounds for which fewer than 10 studies are currently available are not included in the text of this section. The section classifies the attractants in three groups with respect to the three tables, 1) attractive compounds, 2) attractive odors from organisms, and 3) synthetic blends designed to mimic host odors.

Attractive Compounds

Carbon dioxide Carbon dioxide has long been considered to be the most important stimulus mediating attraction in host-seeking behaviour for mosquitoes (Gillies 1980) (Fig. 1). Expired breath from animals contains high levels of carbon dioxide (4% in breath vs 0.035% in atmospheric air) and thus acts for blood-feeding insects as a key signal associated with the presence of a vertebrate host.

Fluctuating levels of CO_2, perceived as intermittent filamentous plumes of CO_2 by mosquitoes, help females to orientate their flight towards the host source (Dekker and Carde 2011; Dekker et al. 2005; Geier et al. 1999b). However a simple exposure to CO_2 also results in flight activation in many mosquito species (Gillies 1980), and detection of CO_2 enhances attractiveness to several host-related olfactory cues, such as OCT (Vythilingam et al. 1992; Kline and Mann, 1998), human skin odors (Dekker et al. 2005; Webster et al. 2015), heat or lactic acid (McMeniman et al. 2014; van Breugel et al. 2015).

Carbon dioxide has been widely used for decades as a mosquito attractant (alone or in combination with other stimuli) in trapping devices and remains among the main olfactory

Table 2 List of odors from living organisms and products derived from animals attractive to adult mosquitoes. Odors are given in alphabetical order. For each odor, studies and effect of the compound are given with respect to mosquito species, which are listed in alphabetical order. Studies that involved only electrophysiological methods (with no behavioural tests) were not included in this table. Studies that only compared the efficacy of different traps were also excluded from the table. For each odor source, the column « co-tested compounds » gives the other compounds that were tested in the study. The column « effect » indicates whether the odor was observed to be attractive alone (Attract.), attractive in combination/synergy with other compounds (Syn. (compound)), synergist for other compounds (Syn.of (compound)), not attractive (No effect), or repellent (Repellent).

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
Calf/cow odor	*Ae. aegypti*	OCT, hand odor, chicken odor	Landing bioassays, SSR	*Attract.*	Majeed et al. (2016)
	An. arabiensis	Cow urine odor	Resting boxes, HLC	Attract. (urine) / No effect	Kweka et al. (2009)
		Human odor, other	Mosquito nets with baits, MMX	No effect	Busula et al. (2015); Dekker and Takken (1998)
		CO_2, human odor	HDT, CDC, OBET, E-nets	Attract.	Abong'o et al. (2018); Duchemin et al. (2001); Kweka et al. (2009)
		CO_2, LA, AM, cow urine	Sticky traps	Attract. (urine)	Hawaria et al. (2016)
		CO_2, human odor, synthetic blend	OBET, E-nets, CDC	No effect	Torr et al. (2008)
	An. atroparvus	CO_2, rabbit odor	2W-olfactom.	No effect	Laarman (1958)
	A. coluzzi	OCT, hand odor, chicken odor	Landing bioassays, SSR	Attract.	Majeed et al. (2016)
	An. funestus	Human odor	OBET	No effect	Duchemin et al. (2001)
	An. gambiae	Human odor	Y-olfactom., OBET, HDT	Attract.	Abong'o et al. (2018); Costantini et al. (1998); Duchemin et al. (2001); Lefevre et al. (2009)
		CO_2, human extracts, LA	2W-olfactom.	Syn. (human odors)	Dekker et al. (2002); Pates et al. (2001)
		CO_2, FO, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	An. melas	CO_2	Ramp traps	Attract.	Gillies and Wilkes (1969); Gillies and Wilkes (1970)
	An. obscurus	CO_2, FO, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	An. stephensi	Human odor	2W-olfactom.	No effect	Omrani et al. (2010)
	An. quadriannulatus	CO_2, human odor	Mosquito nets with baits, OBET, CDC	Attract.	Dekker and Takken (1998); (Torr et al. 2008)
	C. decens	CO_2, FO, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	C. quinq.	CO_2, human odor	Suction traps, CDC, HLT	Attract. / No effect	Kweka and Mahande (2009); Mboera and Takken (1999); Mullens and Gerry (1998)
	M. africana	OCT, hand odor, chicken odor	Standard traps, Landing bioassays, SSR	Attract. / Syn. (CO_2)	Majeed et al. (2016); Reeves (1951)
		CO_2, FO, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
Cheese odor (Limburger)	*An. gambiae*	CO_2, BG-lure	BGS	Syn. (CO_2)	Hoel et al. (2014a)
		FA	Wind tunnel olfactom, EAG	Attract.	Knols and De Jong (1996); Knols et al. (1997)
Cheese odor (synthetic)	*An. gambiae, An. funestus*	CO_2, LA, human odor, hexanoic acid	2W-olfactom.	(Attract.)	Murphy et al. (2001)
Chicken odor	*Ae. aegypti*	Hand odor, 6M5H, Guinea-pig odor	2W-olfactom., landing B., GC-SSR	Attract. / Syn. (CO_2)	Majeed et al. (2016); McBride et al. (2014); McIver (1968)
	An. gambiae, An. arabiensis, An. funestus	FO, cow odor, synthetic blends	Semi-field MMX	Attract. (*arab.*)	Busula et al. (2015)
	C. nigripalpus, C. pilosus	CO_2, rabbit odors	Standard traps	Attract. (*nigripalpus*)	Edman (1979)
	C. pipiens molestus	CO_2, pigeon odor, magpie odor	Flight tube bioassay	Attract. / Syn. (CO_2)	Spanoudis et al. (2020)
	C. quinq.			Attract.	

Table 2 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		CO_2, AM, nonanal, human odor, calf odor	2W-olfactom., ovitraps, GC-EAD, GC-SSR, EVS		Cooperband et al. (2008); Kramer and Mulla (1979); Majeed et al. (2016); Reeves (1951); Syed and Leal (2009)
		CO_2, pigeon odor, magpie odor	Flight tube bioassay	Attract. / Syn. (CO_2)	Spanoudis et al. (2020)
	C. Tarsalis	CO_2, calf odor	2W-cage, standard traps	(Attract.) / Syn. (CO_2)	Mclver (1968); Reeves (1951)
Chimpanzee odor	*An. gambiae*	CO_2, FO, cow odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	An. obscurus	CO_2, FO, cow odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	C. decens	CO_2, FO, cow odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	M. africana	CO_2, FO, cow odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
Goat odor	*An. gambiae*	LA	Trapping huts	Attract. / Syn. (LA)	Kemibala et al. (2020)
	C. quinq.	CO_2, cow/calf odor, human odor	CDC in tents	No effect	Mboera and Takken (1999)
Honey odor	*Ae. aegypti (orco mutants)*	CO_2, human odor, Guinea-pid odor, glycerol	2W-Gouck olfactom.	Syn. (CO_2)	DeGennaro et al. (2013)
	An. gambiae	Soiled socks	Wind Tunnel olfactom.	Attract. (<5 days)	Foster and Takken (2004a)
Human arm/hand odor	*Ae. aegypti*	-	2W- and Y-olfactom.	Attract.	da Silva Paixão et al. (2015); Fernandez-Grandon et al. (2015); Khan et al. (1969); Parker (1948); Schreck et al. (1990); Schreck et al. (1982)
		CO_2	2W- and Y-olfactom.	Attract. / Syn. (CO_2)	Daykin et al. (1965); Dekker et al. (2005); Mayer and James (1969); Schreck et al. (1982); Smart and Brown (1956); Willis (1947)
		CO_2, LA	2W- and Y-olfactom., wind T.	Attract.	Bar-Zeev et al. (1977); Bernier et al. (2007); Eiras and Jepson (1994); Geier and Boeckh (1999); Geier et al. (1996); McMeniman et al. (2014); Smith et al. (1970); Williams et al. (2006b)
		6M5H, other	2W- and Y-olfactom., GCEAD	Attract.	Bernier et al. (2002); Logan et al. (2008); McBride et al. (2014)
		BG-lure, USDA blend, other	Y-olfactom., field BGS	Attract.	Williams et al. (2006a)
		Chicken odor, cattle odor, mammal odor	2W- and Y-olfactom., landing B., GC-SSR	Attract. / Syn. (LA, CO_2)	DeGennaro et al. (2013); Majeed et al. (2016); McBride et al. (2014); Mclver (1968); Steib et al. (2001)
	Ae. albopictus	LA, anisaledhyde, floral compounds	Wind Tunnel	Attract. / Syn. (LA)	Hao et al. (2012); Hao et al. (2013)
	An. arabiensis	CO_2	Wind Tunnel	Attract.	Omer (1979)
	An. coluzzii	Armpit odor, FO, cattle odor	2W-olfactom., landing B., SSR	Attract.	Majeed et al. (2016); Verhulst et al. (2016)
	An. gambiae	Banana ingestion	Exp. cages bioassays	Syn. (Banana ingestion)	Paskewitz et al. (2018)
		AM	2W-olfactom., wind T.	Attract.	Qiu et al. (2006a); Smallegange et al. (2003)
		CO_2, LA, cow odor	2W-olfactom.	Attract. / Syn. (LA)	Dekker et al. (2002)
	An. quadrimaculatus	CO_2	2W-olfactom., test chamber	Attract.	Price et al. (1979); Schreck et al. (1990); Schreck et al. (1982);

Table 2 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
					Willis (1947)
	An. stephensi	Banana ingestion	Exp. cages bioassays	Syn. (Banana ingestion)	Paskewitz et al. (2018)
	C. pipiens	CO_2, fruit odor	2W-olfactom., wind T.	Attract.	Bowen (1992); Omer (1979)
Human armpit extracts	*Ae. aegypti*	-	2W-olfactom.	*Attract.*	Parker (1948)
		CO_2, other	2W-olfactom.	Attract.	Thompson and Brown (1955)
		CO_2, LA, AM, acetic acid	2W-olfactom.	Attract. / No effect	Brown et al. (1951)
	An. coluzzii	FO, hand odor	Three layer 2W-olfactom.	(Attract.)	Verhulst et al. (2016)
Human breath	*Ae. aegypti*	CO_2, arm odor, Guinea-pig odor	2W-Gouck olfactom.	Attract. / Syn. (arm odor)	DeGennaro et al. (2013)
	An. atroparvus	Rabbit blood, cattle blood	2W-olfactom.	Attract.	Laarman (1958)
	A. elutus	Human odor	Experimental cage set-up	Attract.	Mer et al. (1947)
	An. gambiae	CO_2, Ifakara blend	2W-olfactom., wind T., field MMX	Attract. / No effect	Healy and Copland (1995); Lorenz et al. (2013); Mukabana et al. (2004)
Human body odor	*Ae. aegypti*	CO_2, LA, OCT	Field FPT, HLC	Attract.	Canyon and Hii (1997)
	Ae. albopictus	BG-lure, HLC, other	HDN, CDC, BGS, Suna trap	Attract.	Tangena et al. (2015)
	Ae. polynesiensis	CO_2, OCT, BG-lure	BG-S, BG-M, HBC	Attract.	Hapairai et al. (2013)
	An. aquasalis	CO_2	Field CDC, BGS, MM, HLC	Attract.	Hiwat et al. (2011)
	An. arabiensis	CO_2, cow odor	OBET, HLC, host decoy trap	Attract. (cow odor preferred)	Abong'o et al. (2018); Duchemin et al. (2001); Kweka and Mahande (2009)
		CO_2, cow odor, other	OBET, CDC	Attract.	Dekker and Takken (1998); Torr et al. (2008)
		Pregnant women	Nets with women	Attract. (pregnant)	Himeidan et al. (2004)
	A. darlingi	Plasmodium infected people	Vertical olfactom.	Attract. (infected)	Batista et al. (2014)
	An. funestus	-	CDC, exit traps, HLC, MET	Attract.	Knols et al. (1995); Mboera and Takken (1997); Ribbands (1949)
		CO_2	OBET, field MMX	(Attract.) / Syn. (CO_2)	Costantini et al. (1996)
		Cow odor	OBET	Attract.	Duchemin et al. (2001)
		CO_2, LA, FAs	SSAM traps	(Attract.)	Murphy et al. (2001)
	An. gambiae	-	CDC, exit traps, HLC, MET	Attract.	Govella et al. (2016); Hawkes et al. (2017); Knols et al. (1995); Mboera and Takken (1997); Ribbands (1949)
		CO_2	OBET, field MMX	Attract. / Syn. (CO_2)	Costantini et al. (1996); Jawara et al. (2009)
		CO_2, AM, FO, other	2W-olfactom.	Attract.	Olanga et al. (2010)
		Beer consumption	Y-olfactom.	Attract. (beer consumption)	Lefevre et al. (2009)
		Pregnant women	Nets with women	Attract. (pregnant)	Himeidan et al. (2004); Lindsay et al. (2000)
		Plasmodium infected people	3W-olfactom.	Attract. (Plasmodium infected)	Lacroix et al. (2005)
		CO_2, FAs, other	2W-olfactom., OBET	Attract.	Costantini et al. (2001); Murphy et al. (2001)

Table 2 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		Cow/calf odor	Y-olfactom., OBET, HDT, HLC	Attract.	Abong'o et al. (2018); Costantini et al. (1998); Duchemin et al. (2001); Lefevre et al. (2009)
	An. quadriannulatus	CO_2, cow odor, other	OBET, CDC	Attract.	Dekker and Takken (1998); Torr et al. (2008)
	A. marajoara	CO_2	MosqTent, HLS, BGS	Attract.	Lima et al. (2017)
	An. melas		Ramp traps	Attract.	Gillies and Wilkes (1970)
	C. quinq.	-	Men in tents	Attract.	Knols et al. (1995)
		CO_2	OBET, field MMX	(Attract.)	Costantini et al. (1996)
		CO_2, cow/calf odor, goat odor	OBET, HLC, CDC	Attract.	Kweka and Mahande (2009); Mboera and Takken (1999)
Human foot odor	*Ae. aegypti*	CO_2, runk odor, nonanal, octanal, FAs	Field BGS, GC-EAD	Attract.	Owino et al. (2014); Owino et al. (2015)
	An. arabiensis	CO_2, AM, LA, cow odor, SB, other	Field MMX + OBST	(Attract.)	Busula et al. (2015); Hawaria et al. (2016)
	An. coluzzii	AM, Armpit + hand odor	2W-olfactom.	Attract.	De Boer et al. (2017); Verhulst et al. (2016)
	An. farauti	CO_2, BGlure, MB5	Suna traps	Attract.	van de Straat et al. (2019)
	An. gambiae	-	2W-olfactom. + field CFG	Attract.	Andreasen et al. (2004); Omolo et al. (2013); Smallegange et al. (2013); Verhulst et al. (2013)
		CO_2	Landing cage, MMX, BGS	Attract. / Syn. (CO_2)	Hawkes et al. (2012); Schmied et al. (2008); Smallegange et al. (2010); Webster et al. (2015)
		Benzothiazole	2W-olfactom. + GC-EAD	Attract.	Qiu et al. (2004)
		CO_2, AM, LA, OCT	2W-olfactom. + field MMX	Attract. / Syn. (CO_2 + AM)	Njiru et al. (2006); Spitzen et al. (2008); Verhulst et al. (2011b)
		CO_2, AM, LA, FAs	Field MMX	Attract.	Jawara et al. (2011); Murphy et al. (2001)
		Ifaka blend	2W-olfactom. + field MMX	Attract.	Okumu et al. (2010a); Olanga et al. (2010)
		CO_2, Cow odor, SB, MB5	2W-olfactom. + field MMX	Attract.	Busula et al. (2015); Pates et al. (2001)
		Honey	Wind T.	Attract.	Foster and Takken (2004b)
		CO_2, cow odor, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	An. obscurus	CO_2, cow odor, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	An. stephensi		Choice cages	Attract.	Andreasen et al. (2004)
	C. decens	CO_2, cow odor, chimpanzee odor	BGS, Suna traps	Attract.	Bakker et al. (2020)
	C. quinq.	CO_2, acetone, OCT	Wind T., field CFG, CDC	Attract. / Syn. (CO_2)	Lacey and Carde (2011); Lacey and Carde (2012); Mboera et al. (2000c)
Human skin/sweat extracts	*Ae. aegypti*	-	2W-olfactom.	Attract.	Maibach et al. (1966)
		CO_2, LA, hand odor	2W and Y-olfactom., wind T.	Attract.	Eiras and Jepson (1994); Eiras and Jepson (1991); Geier and Boeckh (1999); Geier et al. (1999a); Geier et al. (1996)
	An. gambiae	6M5H, indole, GA	2W-olfactom., EAG	Attract.	Meijerink et al. (2000)
		LA, AM	2W-olfactom.	Attract.	Braks et al. (2001)
		CO_2, LA, FA	2W-olfactom., wind T.	Attract.	Braks et al. (2001); Dekker et al. (2002); Healy and Copland (2000)

Table 2 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		sweat with inoculated axilla bacteria	2W-olfactom.	Attract.	Frei et al. (2017)
	An. stephensi	Guinea-Pig odor, cow odors	2W-olfactom.	Attract.	Omrani et al. (2010)
Mango odors	*Ae. aegypti*	LA, OCT	3cages 2W-olfactom. + field BGS	Syn. (LA + OCT)	Scott-Fiorenzano et al. (2017)
	Ae. albopictus	LA, OCT	3cages 2W-olfactom. + field BGS	Syn. (LA + OCT)	Scott-Fiorenzano et al. (2017)
	An. gambiae	humulene, (E)-caryophyllene and terpinolene	Y-tube olfactom., GC-EAD	Attract.	Meza et al. (2020)
Microbial odors	*Ae. aegypti*	Bacteria associated to Bamboo and Oak leaf infusions	Behav. bioassays	Attract. (GF)	Ponnusamy et al. (2008)
	An. gambiae	Water with bacterial suspensions	2 choice-tests	Attract. (GF)	Sumba et al. (2004)
Mouse/rat odor	*Ae. aegypti*	CO_2, chicken odor	2W-experimental cage	Attract.	McCall et al. (1996); Mclver (1968)
	Ae. albopictus	CO_2, mouse litter odor	Field BGS	Syn. (CO_2)	Le Goff et al. (2017)
		Phenol, 4-methylphenol, 4-ethylphenol, indole	Y-olfactom., BGS	Attract.	Diaz-Santiz et al. (2020)
	An. stephensi	Plasmodium infected mouse	2W-wind Tunnel	Attract.	De Moraes et al. (2014)
Mushroom volatiles	*Ae. aegypti*	Volvariella volvacea, OCT	Y-olfactom.	Attract.	Chaiphongpachara et al. (2019)
	C. quinq.	Pleurotus ostreatus, Thaeogyroporus porentosus, Volvariella volvacea, Pleurotus sajorcaju, and Lentinus edode	Odor-baited resting boxes	Attract. (1 species)	Chaiphongpachara et al. (2018)
	C. sitiens	Volvariella volvacea, Lentinus edodes, OCT	Y-olfactom., resting boxes	Attract.	Chaiphongpachara et al. (2019); Chaiphongpachara et al. (2018)
Plant odor	*Ae. aegypti*	LA, OCT, Mango fruit	3-cages-2W-olfactom., field BGS	Syn. (LA, OCT)	Scott-Fiorenzano et al. (2017)
		CO_2, Tansy and Silene flower extracts,	2W-olfactom., wind T., GC-EAD	Attract.	Jhumur et al. (2007); Peach et al. (2019b)
		Vicia faba honeydew	Y-olfactom., baited traps	Attract.	Peach et al. (2019a)
		Bamboo and Oak leaf infusions	Sticky-screen bioassay, reach-in cage assays	Attract. (GF)	Ponnusamy et al. (2010); Ponnusamy et al. (2008)
		Hay infusion, methyl proprionate	CDC ovitraps	Attract. (GF)	Reiter and Colon (1991)
		Extracts of common milkweed (Asclepias syriaca)	Ew-probing test	Attract.	Vargo and Foster (1982)
		Impatiens walleriana plants	Competition choice test	Attract.	Chen and Kearney (2015)
	Ae. albopictus	LA, OCT, Mango fruit, bamboo and Oak leaf infusions	3-cages-2W-olfactom., field BGS	Attract. (GF) / Syn. (LA, OCT)	Ponnusamy et al. (2010); Scott-Fiorenzano et al. (2017); Trexler et al. (1998)
	Ae. japonicus japonicus	Grass infusion, CO_2, iGu lure, traptech lure,	CDC LT and ovitraps	Attract. (GF) (lures)	Scott et al. (2001)
	Ae. triseriatus	Betula papyrifera infusions, p-cresol	Bioassay cages	Attract. (GF)	Bentley et al. (1979)
	A. albimanus	Brachiaria mutica, Cynodon dactylon, Jouvea straminea, Fimbristylis spadicea, Ceratophyllum demersum	Ovipos. bioassays, wind T.	Attract. (GF)	Torres-Estrada et al. (2005)
	An. arabiensis	Achillea millefolium, Echinochloa pyramidalis, Echinochloa stagnina	2W-ovip., Wind T.	Attract.	Asmare et al. (2017); Healy and Jepson (1988)
		Maize/rice volatiles, 6M5H, limonene, α-pinene, benzaldehyde, nonanal, p-cymene, other	2W-olfactom., BGS, GC-EAD	Attract. (GF)	Wondwosen et al. (2016); Wondwosen et al. (2017)
	An. gambiae	hexanal, β-pinene, limonene, linalool oxide, Parthenium hysterophorus, Bidens pilosa,	2W- and Y-olfactom., wind T, GC-EAD	Attract.	Gouagna et al. (2010); Nikbakhtzadeh et al. (2014); Nyasembe et al. (2012);

Table 2 (continued)

Compound	Mosquito species	Co-tested compounds	Method	Effect	References
		Ricinus communis, Lantana camara, Senna occidentalis, palm wines			Otienoburu et al. (2016); Ugwu and Onwuzurike (2018)
		26 plants tested	Baited glue traps, CDC	Attract. / No effect	Müller et al. (2010)
	C. pipiens	Fruit odors, milkweed flower, hand odor, benzaldehyde, phenylacetaldehyde, (E)-2-nonenal	2W-olfactom.	Attract. / Syn. (3 compounds)	Bowen (1992); Otienoburu et al. (2012)
		Impatiens walleriana plants	Competition choice test	Attract.	Chen and Kearney (2015)
	C. pipiens molestus	Silene flower extracts, phenyl acetaldehyde, veratrole, 2-methoxyphenol, acetophenone, linalool oxide, phenylethyl alcohol	Wind T., GC-EAD	Attract. / Syn. (5 compounds)	Jhumur et al. (2006); Jhumur et al. (2007)
	C. pipiens pallens	Fruit odors, Asclepias syriaca, Abelia chinensis, terpenes	2W-olfactom., box traps	Attract. / Syn. (terpenes)	Ding et al. (2016); Mauer and Rowley (1999); Yu et al. (2019)
		21 plants tested	Multiple choice assays	Attract. / no effect	Yu et al. (2017)
	C. quinq.	Grass infusion, AtrAe. lure, 4-methylphenol, 4-ethyphenol, indole, 3-ethylindole	Bioassay cages, CDC Gravid traps	Attract. (GF) / Syn. (5 compounds) / No effect (AtrAe.)	Gjullin (1961); Gjullin et al. (1965); Irish et al. (2015), (2008); Millar et al. (1992)
	O. japonicus	Grass/hay infusion	Gravid traps	Attract. (GF)	Scott et al. (2001)
Rabbit odor	*An. atroparvus*	CO_2, cattle blood odor	2W-olfactom.	Attract.	Laarman (1958)
	C. nigripalpus, C. pilosus	CO_2, chicken odor	Standard traps	(Attract.)	Edman (1979)
Skin bacteria odors	*Ae. albopictus*	dodecenol, 2-methyl-1-butanol, 3-methyl-1-butanol	Olfactom.	Attract. / Repellent	Michalet et al. (2019)
	An. gambiae	LA, AM, TEA, other	2W-olfactom., MMX traps	Attract.	Verhulst et al. (2010a); Verhulst et al. (2009)

Abbreviations used (Mosquito species): quinq (quinquefasciatus)

Abbreviations used (Compounds): AM (ammonia), CO_2 (Carbon dioxide), DMDS (Dimethyl disulfide), LA (lactic acid), FAs (fatty acids), GA (geranylacetone), 6M5H (6-methyl-5-hepten-2-one), 1-octen-3-ol (OCT), TEA (tetradecanoic acid)

Abbreviations used (Method): 2W-olfactom. (2-way olfactometer), 4A-olfactom. (4-arms olfactometer), Y-olfactom. (Y-olfactometer), Wind t. (wind tunnel), EAG (electroantennography), GC-EAD (gas chromatography/ electroantennodetection), SSR (single sensillum recording). Trap types : BGS (Biogents Sentinel trap), MMX (Mosquito Magnet-X trap), CDC (Centers for Disease Control trap or CDC miniature light trap), CFG (CounterFlow Geometry trap), Obet (Odour-Baited Entry Trap).

Abbreviations used (Effect): GF (Gravid females).

cues associated with mosquito traps used for scientific and public-health purposes worldwide (Wooding et al. 2020).

The addition of a CO_2-release system substantially increases trapping efficacy (CDC traps, Newhouse et al. 1966; Xue et al. 2008; MM-X traps, Njiru et al. 2006; BGS and MM-X traps, Schmied et al. 2008; Roiz et al., 2015). Different sources of CO_2 have been evaluated to find a low-cost, widely applicable and safe CO_2 source: pressurized gas cylinder, dry ice blocks or pellets (Newhouse et al. 1966; Oli et al. 2005), yeast-generated CO_2 (Jerry et al. 2017; Saitoh et al. 2004; Smallegange et al. 2010), propane-derived product (Kline 2002), yeast-fermentation of molasses (Busula et al. 2015; Mweresa et al. 2014), and chemical reactions such as citric acid + sodium bicarbonate, or vinegar + sodium bicarbonate (Hoel et al. 2015). Yeast-generated CO_2 is considered to be the best CO_2 source for odor-baited traps in the field (Smallegange et al. 2010; Jerry et al 2017; Hoël et al. 2015).

More than 93% of the 122 studies that have tested CO_2 attractiveness in the field or under behavioural assays showed a significant increase in mosquito catches or attraction (Table 1). Under field conditions, CO_2 alone enhanced trapping efficacy in 96% of the studies, while adding CO_2 to other attractant components resulted in increased mosquito catches for 84% of the studies. CO_2 was found to be the most

Table 3 List of synthetic blends designed to lure and attract adult mosquitoes. Lure names are given in chronological order, with respect to the year of their invention/publication. Most of the synthetic blends consist of compound mixtures designed to mimic human odors, except for lures designed to attract gravid females to oviposition sites (AtreAedes).

Lure name	Invention	Blend composition	Target species	References
USDA blend	Bernier et al. (2001)	L-Lactic acid + Acetone + Dimethyl disulfide	*Ae. aegypti*	Bernier et al. (2001); Williams et al. (2006a)
AtrAedes lure	Eiras and Santanna (2001) (Agrisense Ltd, Cardiff, UK)	*Panicum maximum* grass infusions	*Ae. aegypti* *Ae. simpsoni* *C. quinq.*	Codeço et al. (2015); da Cruz Ferreira et al. (2017); de Melo et al. (2012); Eiras et al. (2004); Eiras and Santanna (2001); Eiras and Resende (2009); Fávaro et al. (2006); Maciel-de-Freitas et al. (2008); Maciel-de-Freitas and Lourenço-de-Oliveira (2011); Paula et al. (2018); Resende et al. (2012); Resende et al. (2010); Roque and Eiras (2008); Snetselaar et al. (2014) Thornton et al. (2016) Irish et al. (2015); Thornton et al. (2016)
BG-lure	Geier et al. (2004a); Geier et al. (2004b)	L-Lactic acid + Ammonia + fatty acids (including Hexanoic acid). Cartridge (BG-Lure), or sachets (BG-sweetscent)	*Ae. aegypti*	Degener et al. (2019); Kröckel et al. (2006); Liu et al. (2019); Maciel-de-Freitas et al. (2006); Nyasembe et al. (2015); Owino et al. (2014); Rose et al. (2006); Williams et al. (2006a)
			Ae. albopictus	Akaratovic et al. (2017); Bhalala et al. (2010); Crepeau et al. (2013); Degener et al. (2019); Farajollahi et al. (2009); Hoel et al. (2014a); Meeraus et al. (2008); Pombi et al. (2014); Rochlin et al. (2016); Sukumaran et al. (2016); Unlu et al. (2016); Unlu and Farajollahi (2014); Xie et al. (2019)
			Aedes spp.	Nyasembe et al. (2015) (*Ae. mcintoshi, Ae. ochraceus*); Rochlin et al. (2016) (*Ae. Japonicus, Ae. Triseriatus*); Hapairai et al. (2013) (*Ae. polynesiensis*)
			An. arabiensis	Batista et al. (2018); Batista et al. (2017)
			An. darlingi	Batista et al. (2018)
			An. funestus	Batista et al. (2018)
			An. gambiae	Obenauer et al. (2013)
			An. minimus	Ponlawat et al. (2017)
			An. stephensi	Sukumaran et al. (2016)
			C. quinquefasciatus	Batista et al. (2018); Degener et al. (2019); Sukumaran et al. (2016); Xie et al. (2019)
			Culex spp.	Bhalala et al. (2010) (*C. pipiens, C. restuans, C. Salinarius*); Pezzin et al. (2016) (*C. pipiens*)
Synthetic Blend (SB)	Smallegange et al. (2005)	Ammonia, Lactic acid, 12 carboxylic acids	*An. gambiae*	Smallegange et al. (2005)
Lurex / Lurex 3	Hoel et al. (2007) (first use of Lurex lactic acid cartridges)	L-Lactic acid	*Ae. aegypti*	Degener et al. (2019)
			Ae. albopictus	Degener et al. (2019); Hoel et al. (2007); Li et al. (2010); Xue et al. (2010)
			An. crucians	Xue et al. (2010)
			A. darlingi	Vezenegho et al. (2014)
			An. gambiae	Kitau et al. (2010)
			An. sinensis	Li et al. (2010)
			C. nigripalpus	Hoel et al. (2007); Xue et al. (2010)

Table 3 (continued)

Lure name	Invention	Blend composition	Target species	References
			C. quinquefasciatus	Degener et al. (2019); Xue et al. (2010)
			Culex spp.	Li et al. (2010) (*Culex tritaeniorhynchus, Cx. pipiens pallens*); Hoel et al. (2007) (*C. nigripalpus, C. erraticus*).
Synthetic Blend 2 (SB)	Smallegange et al. (2009)	Ammonia, Lactic acid, Tetradecanoic acid	*An. arabiensis, An. funestus*	Busula et al. (2015)
			An. gambiae	Busula et al. (2015); Smallegange et al. (2009)
Ifakara blend	Okumu et al. (2010b)	Carbon dioxide, Ammonia (2.5%), L-Lactic acid (85%), Propionic acid (C3) 0.1%, Butanoic acid (C4) 1%, Pentanoic acid (C5) 0.01%, 3-Methylbutanoic acid (3mC4)	*An. arabiensis*	Lorenz et al. (2013); Matowo et al. (2016)
			An. funestus	Batista et al. (2018); Mweresa et al. (2015)
			An. gambiae	Batista et al. (2018); Lorenz et al. (2013); Okumu et al. (2010a); Okumu et al. (2010b); Olanga et al. (2010)
			Culex spp.	Batista et al. (2018); Mweresa et al. (2015); Okumu et al. (2010b)
			Mansonia spp.	Batista et al. (2018); Mweresa et al. (2015); Okumu et al. (2010b)
Mbita blend / MB5	Menger et al. (2014b); Mukabana et al. (2012b)	3-Methyl-1-butanol, Tetradecanoic acid, Ammonia, (S)-Lactic acid, and Carbon dioxide MB5 = Mbita blend + Butan-1-amine	*Ae. aegypti*	Verhulst et al. (2015)
			Ae. albopictus	Pombi et al. (2014)
			Ae. arabiensis	Busula et al. (2015)
			An. coluzzii	Cribellier et al. (2018); Verhulst et al. (2015)
			An. funestus	Batista et al. (2018); Busula et al. (2015); Homan et al. (2016)
			An. gambiae	Batista et al. (2018); Busula et al. (2015); Hiscox et al. (2014); Mukabana et al. (2012b); Mweresa et al. (2016)
			C. pipiens	Batista et al. (2018); Verhulst et al. (2015)
TrapTech Lure / iGu	Bedoukian Research, Inc., Danbury, CT. First study : Anderson et al. (2012)	250 mg of R-1-Octen-3-ol and 1900 mg of Ammonium bicarbonate	*Ae. aegypti*	Thornton et al. (2016)
			Ae. albopictus	Rochlin et al. (2016); Unlu et al. (2016)
			Ae. triseriatus	Rochlin et al. (2016)
			Ae. japonicus	Anderson et al. (2012); Balestrino et al. (2016); Rochlin et al. (2016); Wagner et al. (2018)
			Ae. geniculatus	Wagner et al. (2018); Wagner and Mathis (2016)
			Aedes spp.	Thornton et al. (2016) (*Ae. simpsoni*); Wagner et al. (2018) (*Ae. annulipes/cantans, Ae. sticticus, Ae. vexans*)
			C. quinquefasciatus	Thornton et al. (2016)
Honad lure	Tchouassi et al. (2013)	Heptanal, Octanal, Nonanal, Decanal	*Ae. aegypti*	Nyasembe et al. (2015)
			Ae. mcintoshi, Ae. ochraceus	Nyasembe et al. (2015); Tchouassi et al. (2013)
			An. gambiae	Jacob et al. (2018)
Mix-5	Xie et al. (2019)	Heptanal, Octanal, Nonanal, Decanal	*Ae. albopictus, C. quinquefasciatus*	Xie et al. (2019)

important synergist for many candidate attractants, such as ammonia (Hawaria et al. 2016; Njiru et al. 2006; Spitzen et al. 2008), lactic acid (Eiras and Jepson 1991; El-Sisi et al. 2019; Hoel et al. 2007; Spitzen et al. 2008; Verhulst et al. 2011a), linlool oxide (Nyasembe et al. 2015), 3-methyl-1-butanol (Menger et al. 2014b; van Loon et al. 2015), OCT

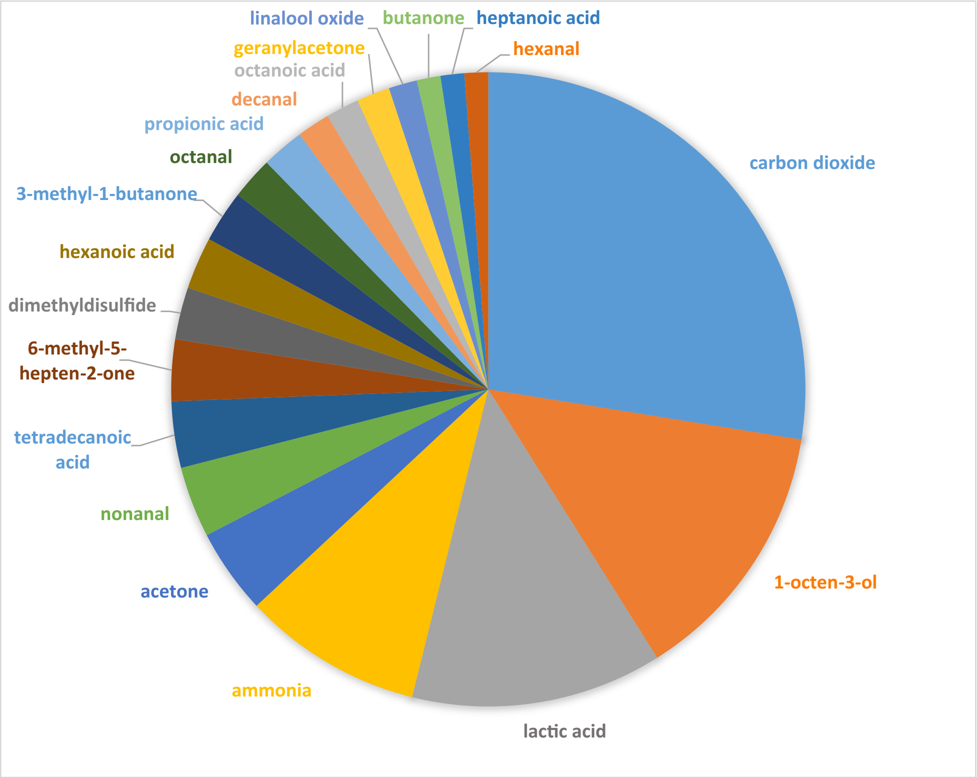

Fig. 1 Distribution of studies in which the compound investigated was found to be attractive to mosquitoes (n = 316 studies)

(Hapairai et al. 2013; Kline et al. 1991b), or tetradecanoic acid (Van Loon et al. 2015).

Lactic Acid The attractiveness of L-lactic acid (or 2-hydroxypropanoic acid, hereafter LA) was first reported following chemical analyses of the acidified fraction of forearm-washing extracts, and after exposure of *Aedes aegypti* females to this compound in an olfactometer. Humans and other vertebrates naturally produce the levorotatory isomer of lactic acid, L-lactic acid, while the presence of D-lactic acid in body fluids usually results from bacterial infections (Smith et al. 1986).

LA is a by-product of glycolysis in many animals, generated from pyruvic acid under anaerobic conditions in various tissues, such as muscles, brain, kidney, or red blood cells (Gladden 2004). Because LA has low volatility, body emanations of this compound are linked to its high concentration in sweat (Derbyshire et al. 2012). LA is majoritarily produced within eccrine-sweat glands, whose density on human skin surfaces is markedly higher than in all other mammals (Best et al. 2019; Montagna 1985). Comparing the amounts of LA emissions from the skin surface of humans and several other mammals, Dekker et al. (2005) found concentrations of LA at least five times higher in samples from humans than in those from other mammals. Consequently, the high levels of this compound released from the human body have been hypothesized to represent a specific human host-recognition cue for anthropophilic mosquitoes (Dekker et al. 2005; Steib et al. 2001). For example, addition of LA to non-attractive mammal odors dramatically increases their attractiveness to *Ae. Aegypti* (Steib et al. 2001). Moreover, LA may also emanate from human breath (Jackson et al. 2017; Marek et al. 2010). The respective parts of LA release from breath *versus* from sweaty skin remain unknown so that global LA emissions from a vertebrate cannot be concluded yet as a strict human-specific signal for anthropophilic mosquitoes (Dekker et al. 2002). In humans, variation among persons in the production of LA is suspected to play a key role in determining attractiveness to mosquitoes (Acree et al. 1968; Dekker et al. 2002; Smith et al. 1970).

LA has rarely been reported to be efficient alone, but rather acts in combination or synergistically with carbon dioxide or other compounds (Acree et al. 1968). For example, *Ae aegypti* has been observed to be attracted by LA alone (Geier and Boeckh 1999; Geier et al. 1996), whereas LA is attractive to *An. gambiae* only in combination with CO$_2$ or ammonia (Dekker et al. 2002; Smallegange et al. 2005) and attractive to *Ae. albopictus* only when combined with OCT (Hoel et al. 2007). Among the 49 studies that evaluated the effect of LA on mosquito attractiveness in the laboratory or in the field, 42 (86%) reported an attractive effect or an increased number of mosquito catches when this compound was combined with other attractants (Table 1).

LA is a regular component of synthetic blends or lures that have been developed to increase mosquito trapping in the field (see Table 3). A repellent effect of LA for adult mosquitoes has been reported in a few studies (Brown et al. 1951; Rudolfs 1922; Shirai et al. 2001).

Ammonia Ammonia was initially examined as a possible attractive compound by several authors (Rudolfs 1922; Reuter 1936; Brown et al. 1951), but no effect on mosquito orientation was found until Geier et al. (1999a) tested ammonia in combination with lactic acid, and found a strong additive effect. Although most later authors found ammonia to be active only when other compounds are present (synergy with lactic acid, tetradecanoic acid, or CO_2), a few studies showed that ammonia presented alone can significantly attract mosquitoes, including *Ae. aegypti* (Mathew et al. 2013) and *An. gambiae* (Braks et al. 2001).

Ammonia is constantly produced in various tissues of the body of living organisms, mainly as a result of amino-acid catabolism (Walker 2014). The presence of ammonia in human body odors can be detected both in exhaled breath and skin emanations, but the respective parts of these emissions have not yet been compared in detail (Geier et al. 2002). The level of ammonia in sweat is strongly linked to the amounts of plasma ammonia (Czarnowski et al. 1992), while ammonia in breath may originate from different sources (Chen et al. 2014).

Ammonia has been successfully included in the composition of most of the modern synthetic lures used in field trap systems, such as in the "Synthetic blend" (Smallegange et al. 2005), the BG-Lure (Geier et al. 2004a,b), the Ifakara blend 1 (Okumu et al. 2010b), the Mtiba blend (Mukabana et al. 2012b), and the Mix-5 (Xie et al. 2019) (see Table 3).

***1-octen-3-ol* (OCT)** OCT, also known as the "mushroom alcohol", is a natural compound typically produced and emitted by fungi. It derives from the enzymatic oxygenation of linoleic acid (Wurzenberger and Grosch 1984), and has been identified in the volatiles of many mushroom species (Dickschat 2017), but also in the flower scent of numerous plant species (Knudsen et al. 2006) and volatiles from bacteria (Davis et al. 2013). The presence of OCT in mammal body odors was first documented by Hall et al. (1984), who analyzed the volatiles emitted by oxen. OCT has been identified as a natural ligand of the bovine odorant-binding protein present in the respiratory and olfactory nasal mucosa of ruminants (Ramoni et al. 2001).

Although OCT is sometimes regarded as a component of human sweat or exhaled breath, its presence in human body odors remains to be demonstrated. While more than 90 studies have already investigated the composition of exhaled breath and human skin odors (see the reviews of Dormont et al. 2013, Lawal et al. 2017, and more recent papers), only three studies have detected the presence of 1-octen-3-ol in skin volatile extracts (Bernier et al. 2000; Cork and Park 1996; Gallagher et al. 2008).

The efficacy of OCT as an insect attractant was first reported by Hall et al. (1984) for tsestse flies. Takken and Kline (1989) demonstrated that OCT can also be used as a mosquito attractant, and found increased catches of host-seeking mosquitoes such as *Aedes* or *Anopheles* species, while *Culex* species were observed to be only weakly attracted to OCT (Kline et al. 1991a; Kline 2007). For example, OCT is particularly efficient in attracting *Ae. Albopictus* (Qualls and Mullen 2007; Roiz et al. 2016), whereas OCT-baited traps failed to catch *C. quinquefasciatus* (Majeed et al. 2016; Mboera et al. 2000c) and other *Culex* species (Essen et al. 1994; Kemme et al. 1993; Kline 2007). OCT may even have a repellent effect for some species, such as *C. quinquefasciatus* (Xu et al. 2015) and (at high doses) *Ae. Albopictus* (Guha et al. 2014). Interestingly, OCT and CO_2 unequivocally act synergistically in field trapping experiments (Kline et al. 1991a, b; Kline and Mann 1998) whereas OCT is often found not to be attractive by itself (Kline et al. 1991a; Rueda et al. 2001; Russell 2004; Shone et al. 2003; Vythilingam et al. 1992). OCT has thus been widely used for the trapping of mosquitoes since the 1990's, and 36 of the 48 studies (75%) that evaluated OCT efficacy in the field found a significant increase in mosquito catches (Table 1). Both (R)- and (S)- enantiomers of OCT were found effective in catching mosquitoes in the field, but (R)-1-octen-3-ol was more attractive than the isomeric mixture (Kline et al. 2007), confirming observations that olfactory receptor neurons are more sensitive to this enantiomer (Bohbot and Dickens 2009).

Surprisingly, this attractive compound is not included in the synthetic blends or commercial lures developed for the trapping of mosquitoes, except the TrapTech lure (Table 3). However, OCT is the principal component provided with a few commercial traps, such as the Dragonfly or MM-X traps (Kline 2006).

Fatty Acids Carboxylic acids, and particularly fatty acids (FAs) (carboxylic acids carrying an aliphatic chain), have long been suspected to be attractive compounds for mosquitoes. Both short-chain (C2-C5) and medium-chain (C6-C11) FAs are commonly found in volatile emissions from human skin (Ara et al. 2006; Caroprese et al. 2009; Dormont et al. 2013). Volatile FAs in skin odors originate from the metabolism of glycerol, lactic acid, amino acids, and diverse skin lipids, under the action of various skin bacteria (James et al. 2004; James et al. 2013). Interestingly, the presence of volatile FAs emanating from skin host may serve as a chemical signature for host-seeking anthropophilic mosquitoes to locate a human host: other hosts such as non-human mammals or birds do not emit such volatile compounds (Nicolaides et al. 1968).

Rudolfs (1922) and Reuter (1936) were the first to imagine the possible effects of some C2-C6 FAs on mosquito behaviour. However, the first demonstration of FAs activity on adult mosquitoes was made much later, by Carlson et al. (1973), who screened the attractiveness of numerous acids for *Ae. aegypti* females. Many FAs have since been shown to attract diverse species of mosquitoes (Puri et al. 2006; Seenivasagan et al. 2014; Smallegange et al. 2009) (see Table 1), and have been successfully used, individually or in FAs blends, as attractive lures for field trapping (Jawara et al. 2011). For instance, several FAs have been incorporated in the formulation of widely used synthetic blends designed to mimic human odor in the field, such as ifakara blend (which includes C3 to C5 FAs), Mbita blend (which includes tetradecanoic acid), or BG-lure (in which hexanoic acid is the dominant compound) (see Table 3).

Natural Host Odors

Human Odors The crucial role of human body odors was early suspected, following observations showing that some mosquito species are preferentially attracted to human hosts and rely on human odors to detect and select their host (Takken 1991). Because several mosquito species bite some parts of the body more frequently than others (De jong and Knols 1995), several body regions have been studied to evaluate their relative attractiveness to host-seeking mosquitoes. Hands and feet odorare among the most frequent body parts whose odors have been included in behavioural bioassays (see Table 2). Tests using armpit sweat extracts, other skin sweat extracts, or breath volatiles, have also been conducted to elucidate the effects of human body odors. Some studies have even tested the attractiveness to mosquitoes of odor of the entire human body, under laboratory conditions using olfactometer devices (Lacroix et al. 2005; Lefevre et al. 2009; Olanga et al. 2010) or under field conditions using diverse trapping methods (Table 2).

Most studies using human odors as stimuli to attract host-seeking mosquitoes have reported a strong and significant attractive effect, at least for mosquito species exhibiting a high degree of anthropophily: for both *Ae. aegypti* and *An. gambiae*, 100% of studies have found human odor samples very effective in attracting mosquitoes. Among odors emanating from various body parts, foot odors have been demonstrated to be highly attractive to several anthropophilic mosquitoes (De Jong and Knols 1995; Dekker et al. 1998; Lacey and Carde 2011). Following such observations, Njiru et al. (2006) demonstrated that traps baited with nylon socks worn by human subjects were very efficient in catching adult mosquitoes under field conditions. Other authors have also successfully used traps baited with nylon socks to collect mosquitoes (Jawara et al. 2009; Qiu et al. 2004; Schmied et al. 2008; Smallegange et al. 2010). Foot odors consist of numerous volatile compounds and particularly include various FAs (Ara et al. 2006; Caroprese et al. 2009) that have been shown to elicit strong olfactory responses of female mosquitoes (Meijerink and van Loon 1999; Smallegange et al. 2009).

Most of the synthetic blends used to enhance trapping efficiency in the field consist of mixtures mimicking human odors, and thus include components that have been chemically identified from volatile skin or sweat samples (Table 3). Such lures often involve compounds such as lactic acid, ammonia, aldehydes, and diverse FAs, all of which have been recorded in human skin odors and observed to elicit mosquito behavioural and electrophysiological responses.

Interestingly, differences in attractiveness among persons have long been known. For example, in several early studies, babies and children were observed to be less bitten than adults (Carnevale et al. 1976; Clyde and Shute 1958; Muirhead-Thomson 1951a; Thomas 1951), while pregnant women have been shown to attract more host-seeking mosquitoes than other women (Ansell et al. 2002; Himeidan et al. 2004; Lindsay et al. 2000). Several authors have also recorded clear variation in attractiveness to female mosquitoes among individuals that cannot be accounted for by such differences in age and reproductive state (Burkot 1988; Curtis 1986; Knols et al. 1995; Lindsay et al. 1993; Michael et al. 2001; Scott et al. 2006). Such heterogeneity in human-mosquito interactions is suspected to result from differences in human odor profiles (Bernier et al. 2002; Geier et al. 2002; Logan et al. 2008). However, chemical explanations for the differences in attractiveness among distinct human odor profiles remain to be established. Among the main components currently isolated in skin emanations, the ratio of two terpenes 6-methyl-5-hepten-2-one ("sulcatone") and geranylacetone has been hypothesized to partly explain why some people are more attractive to mosquitoes than others (Leal et al. 2017; Logan et al. 2010). 6-methyl-5-hepten-2-one is even considered to be a key attractant that leads *Ae. aegypti* to preferentially bite human hosts (McBride et al. 2014). The relative proportions of aldehydes such as nonanal, decanal, or octanal, which are regularly found in skin volatile extracts (Dormont et al. 2013), have been also proposed to play a key role in the attraction of anthropophilic mosquitoes (Jacob et al. 2018; Leal et al. 2017; Owino et al. 2015; Syed and Leal 2009). Other authors have considered L-lactic acid to be a key compound in which inter-individual variation in levels emitted could explain the differential attractiveness that is frequently observed (Dekker et al. 2002). Mukabana et al. (2004) suggest that the breath of some individuals contains repellent compounds, perhaps explaining why some humans are bitten more than others.

However, why some persons attract more host-seeking mosquitoes than others is still not fully understood. Investigating this question requires a detailed examination of the chemical composition of human odors, but analysis of skin volatiles remains complex and is often subject to uncertainties in identification (Charpentier et al. 2012; Dormont et al. 2013).

More recently, the key role of commensal cutaneous microorganisms, i.e. skin microbiota, in human attractiveness to mosquitoes has been highlighted by some authors (Braks et al. 1999; Braks and Takken 1999; Busula et al. 2015; Takken and Verhulst 2017; Verhulst et al. 2010b). Human-associated microbiota living on the skin have been shown to strongly influence the production of skin volatiles, which contain both volatile compounds of microbial origin and bacteria-transformed compounds of sweat origin. Variation in the distribution of skin bacteria on the human body, which is mainly linked to the local abundance of skin glands of different types (Kearney et al. 1984), may explain the differences in body odor composition among body parts. For example, the strong odor emanating from feet (Ara et al. 2006; Caroprese et al. 2009), which is highly attractive to host-seeking mosquitoes (De Jong and Knols 1995; Dekker et al. 1998), is likely determined by the specific and unique microbiota populations associated with this body part (Adamczyk et al. 2020). At the same time, the varying composition of skin microbiota among human subjects (Byrd et al. 2018; Fierer et al. 2008; Grice et al. 2009) may likely contribute to the differences of human odors among subjects, and thus to the differences in human attractiveness to mosquitoes. To summarize, the human skin microbiota likely play a crucial role in the formation of human body odors, and thus in the chemical ecology of anthropophilic mosquitoes searching for a human host (Verhulst et al. 2010a, 2011a, b; 2010b).

Cow Odors Among odors from diverse animals that have been tested to attract mosquitoes, such as those of birdsodor (Spanoudis et al. 2020; Syed and Leal 2009), or of the mouse odor(Le Goff et al. 2017; McCall et al. 1996), volatile emissions from cows and their effects on mosquito attractiveness have been investigated by many authors (Table 2). Cow odors were found to be equally attractive to human odors for host-seeking adult females of anthropophilic species, such as *Ae. aegypti* (Majeed et al. 2016) and *Ae. arabiensis* (Abong'o et al. 2018; Duchemin et al. 2001). Adult females of *Mansonia africana* were observed to prefer cow odors to odors of several other mammalian odors (Bakker et al. 2020). Even for mosquito species known to prefer cow over man for blood meals, e.g. for the zoophilic *A. quadriannulatus*, the attractive effects of cow odors in host-seeking behaviour were found to be as great as that of CO_2, suggesting that the dominant role of host odors relative to that of CO_2 characterizes only anthropophilic mosquito species (Dekker and Takken 1998).

Plant Odors Volatiles from plants represent another source of odors that have a great potential to serve as mosquito attractants. Mosquitoes may be guided towards plant-originated odors for two main reasons: when searching for sugar sources (usually floral nectar) (Foster 1995; Takken and Knols 1999) or oviposition sites (Afify and Galizia 2015; Mwingira et al. 2020; Wooding et al. 2020). In both cases, olfactory cues emanating from plants, e.g. floral volatiles or odors from grass-infused water, play a major role in attraction of adult mosquitoes.

Regarding sugar feeding, many species of mosquitoes are attracted by floral volatiles from diverse angiosperm species (Barredo and DeGennaro 2020; Nyasembe and Torto 2014) (and see Table 2). Whole flower extracts, as well as fruit odors, have been shown attractive to several mosquito species. Single volatile compounds emanating from floral or vegetative plant parts have been also shown to be behaviourally active as mosquito attractants, such as diverse terpenes, fatty acid derivatives, or even green leaf volatiles (Jhumur et al. 2007; Nyasembe and Torto 2014; Wooding et al. 2020). Interestingly, some terpenes, which are naturally not produced by mammals have recently been isolated in the odors of malaria-infected mammals and were hypothesized to explain the enhanced host attractiveness of infected individuals to mosquitoes (Emami et al. 2017; Kelly et al. 2015). Sugar feeding concerns Both males and females feed on sugar sources and identifying the attractants mediating this behaviour may be of high interest if new mosquito control strategies require trapping of males.

The selection of oviposition sites has been demonstrated to be mediated by several olfactory cues, such as specific pheromones, emanations from larvae, pupae, and eggs, and also compounds of bacterial or plant origin (Afify and Galizia 2015; Mwingira et al. 2020; Wooding et al. 2020). Emanations from grass or hay infusion have been shown to attract gravid females of several mosquito species. Electrophysiological and behavioural tests with various plant-produced volatile compounds, or molecules of bacterial origin from water containing fermenting leaves (Ponnusamy et al. 2008), revealed some molecules involved in oviposition site selection by female mosquitoes. For example, compounds such as 4-methylphenol, 4-ethylphenol, indole, phenol, or 3-methylindole are attractive to females searching for oviposition sites in *Ae. aegypti* (Baak-Baak et al. 2013)*, Ae. albopictus* (Diaz-Santiz et al. 2020), *Ae. triseriatus* (Bentley et al. 1979) and *C. quinquefasciatus* (Beehler et al. 1994; Millar et al. 1992). In other cases, blends of terpenes were found to attract gravid females, such as in *A. arabiensis* (Wondwosen et al. 2016).

Synthetic Blends

The efficacy of mosquito traps primarily relies on the effectiveness of the odor bait released by the trapping device. Decades of research on mosquito attractants have highlighted some isolated chemical compounds that are very effective in luring and catching flying adult mosquitoes, as well as other compounds weakly attractive on their own, but that proved biologically very active in combination with other molecules.

In the meantime, constant progress in the analysis of the chemical composition of human body odors has provided many other interesting compounds to be evaluated for their potential attractiveness to mosquitoes. Several authors have developed mixtures of synthetic compounds designed to mimic naturally-emitted odors of a human body. Such synthetic blends generally include volatile compounds identified to be specifically emitted by skin (e.g. free fatty acids), together with compounds found to occur in significantly higher levels in odors of humans compared to those of other animals (e.g. lactic acid).

A first candidate blend, including lactic acid, acetone, and dimethyl disulphide, and referred to as “USDA blend”, was proposed by Bernier et al. (2001) (Table 3). This first blend was found to be an attractive odor to *Ae. aegypti* as human odor in olfactometer bioassays (Williams et al. 2006a). Most of the synthetic blends subsequently developed to mimic human scent contain two main attractive components, lactic acid and ammonia, except Lurex, which only consists of lactic acid (Table 3). The blends mainly differ by the composition of carboxylic acids added to the mixture. Among the three most often used synthetic blends—BG-lure, ifakara blend, and Mbita blend—the first one remains the most widely-used lure chosen for odor-baited trapping studies on mosquitoes. To date, BG-lure has been included in 29 studies, while the ifakara and Mbita blends have been used in 10 and 12 studies, respectively. The BG-lure has proven effective in catching 17 different mosquito species, as well as other insect species (Ortiz et al. 2020). This artificial lure, which is presented as an « artificial human skin scent », consists of a blend of ammonia, lactic acid, and hexanoic acid in specific proportions (Geier et al. 2004a, b; Kröckel et al. 2006), and is currently proposed with the commercial Biogents® Sentinel mosquito trap (Biogents GmbH, Regensburg, Germany) as the “BG-Sweetscent”, in which synthetic compounds are contained within sachets instead of cartridges for the BG-lure.

Surprisingly, OCT, which has long been considered a promising mosquito attractant, is not a component of the synthetic attractive blends listed in Table 3, except for one, the TrapTech lure. OCT has often been tentatively used as an attractant lure in experimental field trapping, with contrasting results for different target mosquito species (Table 1). However, some authors reported OCT to be a strong and effective attractant for mosquitoes such as *Ae. albopictus* (Li et al. 2010; Qualls and Mullen 2007), *Ae. taeniorhynchus* (Kline et al. 1991b; Takken and Kline 1989), and *A. darlingi* (Vezenegho et al. 2014), and this compound is now successfully used in trapping diverse mosquito species over the world (Duffield et al. 2019; Evans et al. 2019; Ibáñez-Justicia et al. 2020; Ortega-Morales et al. 2019). The commercially available traps of Mosquito magnet® (Woodstream Corp., Lancaster, PA 17602) are proposed with OCT as the main attractant lure.

Perspectives

More knowledge about the compounds attractive to mosquitoes is undoubtedly needed to further improve the efficiency of baited-traps for mosquito surveillance and control. Identifying the most attractive compounds or blends of compounds, and characterizing the concentrations and ratios that result in the greatest activity, remains to be done for many mosquito species that are vectors of diseases.

Understanding how adult mosquitoes are attracted to volatile signals also requires improving our knowledge of mosquito olfaction. The molecular mechanisms of compound detection by odorant receptors in mosquitoes have been investigated in diverse mosquito species, and recent findings, such as those of Degennaro et al. (2013), McBride et al. (2014), Raji et al. (2019), and Duval et al. (2019), may have promising applications for the use of semiochemicals in vector control programs.

Recent findings showing that mosquitoes are more attracted to malaria-infected than to uninfected hosts may help us find new candidate attractant molecules. Indeed, enhanced attractiveness to adult mosquitoes linked to a change in host odors after an infection has been observed for several models, including humans (Lacroix et al. 2005; Robinson et al. 2018), birds (Cornet et al. 2013; Diez-Fernandez et al. 2020) and mice (De Moraes et al. 2014). Several volatile compounds associated with malaria infection have been identified (De Boer et al. 2017; De Moraes et al. 2018; Kelly et al. 2015; Robinson et al. 2018) and such investigations may facilitate the discovery of new mosquito-attractive compounds in the future. Another way to find new attractive compounds is to conduct studies on mosquitoes other than anthropophilic species: the great majority of studies listed in this review deal with mosquito species that bite humans. Research programs focusing on the chemical ecology of zoophilic mosquito species would probably help us identify interesting new chemical attractants.

Another key point in the use of attractive odors is the design of odor dispenser devices that will deliver volatile compounds under precise conditions. Delivery techniques should ensure constant release rates of attractants in the appropriate amounts (and for blends, in the appropriate proportions) and permit odor delivery over a long period.

Different delivery methods have been developed and used in odor-baited traps, such as low-density polyethylene (LDPE) sachets (Jawara et al. 2011; Torr et al. 2008), nylon strips (Mukabana et al. 2012a; Mweresa et al. 2015; Okumu et al. 2010a), and classic glass vials (Costantini et al. 2001). However, these dispensing devices have often been evaluated based on their efficiency in catching host-seeking mosquitoes, but have not been examined in terms of the chemical composition of the odor released and its stability over a prolonged period of use. Another promising method has been recently developed, which consists of putting synthetic compounds into a glass vial sealed with a polytetrafluoroethylene/rubber septum, in which is inserted a micro-capillary tube. Such a device ensures a regular amount of volatile emissions, and release rates can be calibrated by the length and the diameter of the capillary tube (Erb et al. 2015; Proffit et al. 2020).

Further investigations should also address more precisely the different contexts (adult life stages) in which adult mosquitoes are guided by attractive volatile cues. While it is now well known that distinct odor signals are used by mosquitoes searching for mates, sugar meals, hosts, or oviposition sites, a large majority of studies have focused on chemical signals mediating host-seeking behaviour (254 of the 316 studies, Tables 1 and 2). Most of the currently available commercial traps rely on odor blends used by flying mosquitoes looking for hosts, and 10 of the 11 synthetic blends listed in Table 3 are designed to attract host-seeking mosquitoes. However, a list of semiochemicals attractive to females searching for oviposition sites is now available (Table 1). Targeting gravid female adults searching for oviposition sites by using Autocidal Gravid Ovitraps (Mackay et al. 2013) under mass trapping programs may allow a consequent reduction of mosquito female populations (Barrera et al. 2014; Lega et al. 2020).

Reducing the density of mosquito local populations and reducing the survivorship of adult females, in particular in risk areas of virus transmission, by attracting adult females to odor-baited traps is now considered to be a valuable complementary vector control method. The use of lure-and-kill traps, or the recent development of mass trapping, have proved effective in durably decreasing vector populations in some cases (Degener et al. 2014; Johnson et al. 2017) and it is expected that the use of mosquito attractants will have an increasingly important role to play in integrated vector control strategies.

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