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Review Article

Chemical Cues for Malaria Vectors Oviposition Site Selection: Challenges and Opportunities

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The attractiveness of oviposition site for malaria vector mosquitoes is dependent upon a number of physical and chemical factors. Many aspects of mosquito behavior, including host location and oviposition, are mediated by volatile semiochemicals. It is anticipated that selection of oviposition site by semio-chemicals in the form of attractants or stimulants can be used in oviposition traps to monitor or possibly in combination with insecticides to control gravid mosquito populations for mass trapping. So far, volatile compounds identified as oviposition attractants for mosquitoes include phenol, 4-methyl phenol, 4-ethyl phenol, indole, skatole, and p-cresol from hay infusions; 3-carene, α-terpinene, α-copaene, α-cedrene, and d-cadinene released by copepods; alcohol and terpenoids including p-cresol from plants; ethyl acetate and hydrocarbon substances, probably released by filamentous algae; 3-methyl-1-butanol identified from bacteria. Research priorities should be directed at identifying more oviposition attractants to determine the properties of these semio-chemicals for possible use in designing control tools. This would aim at luring females to lethal traps or stimulants to increase their exposure to insecticide-impregnated substrates.

1. Background

Malaria is one of the most significant and debilitating insect-transmitted human diseases and has infected humans for over thousand years and may have been a human pathogen for the entire history of mankind [1]. Today, malaria causes about 225 million cases of fever and approximately 600,000 deaths annually more specifically in children under age of 5 years [2]. This represents at least one death (child) every 39 seconds and 85–90% of the deaths occur in sub-Saharan Africa [2].

Mosquitoes spend the first part of their lifecycle in aquatic habitats [3]. The choice of an appropriate oviposition sites has significant impact on the fitness of progeny, distribution of larvae, population dynamics, and the overall maternal reproductive fitness and success [4, 5]. Oviposition process requires complex integration of physical and chemical cues by gravid mosquitoes. Long-range cues, probably involving vision, allow mosquitoes to identify different habitats and oviposition site characteristics. As mosquitoes approach an oviposition site other cues such as phenol, 4-methyl phenol, 4-ethyl phenol, indole, skatole, and p-cresol from hay infusions; 3-carene, α-terpinene, α-copaene, α-cedrene, and d-cadinene become important. Once oviposition site is identified, short-range cues become increasingly important. Short-range cues include temperature and chemical signals received by contact chemoreceptors [6].

Electrophysiological studies have demonstrated that as the blood meal is digested in *Aedes aegypti*, neurons sensitive to host-produced cues, such as lactic acid, become less sensitive, while neurons sensitive to oviposition site attractants, such as methyl butyrate, become more sensitive [7]. Understanding oviposition sites is therefore important to behavioral and vector ecologists because of its potential use in developing successful vector control strategies for insect-borne infectious diseases [8]. A comprehensive knowledge of variations in oviposition behaviors and identification of their determinants that can be used as a repellant or attractant is a key step in this process.

2. Mosquito Oviposition Site Selection

2.1. Role of Habitat Characteristics. Oviposition site selection is the net result of the interaction of a complex array of both chemical and physical factors. The potential breeding sites of anopheline mosquito vectors differ in a range of characteristics, both biotic and abiotic [9, 10]. Anopheline mosquitoes, particularly *An. gambiae s.l.*, actively select habitats for enhancing survivorship and development of immature stages [11]. The source of these physical and chemical signals associated with these breeding sites act as important mediating factors.

The characteristics of potential breeding sites either singly or synergistically influence oviposition of gravid mosquitoes [12]. This occurs through several sensor factors including olfactory [13], tactile, temperature, chemical, and visual cues [6, 14]. Chemical cues may be sensed before physical contact with the site, or they may be sensed upon contact [15] and may emanate from a variety of sources, including microorganisms; mosquito eggs, larvae, or pupae; decomposing organic materials; microbes of larval breeding water and predators or competitors, whether vertebrate or invertebrate [5, 6, 16–23]. Physical characteristics of water collections and their surroundings are assessed by gravid females for long-range identification of potential breeding sites, including color, optical density, reflectance, and temperature [24–26]. Certain physical factors influencing oviposition of *Anopheles gambiae* Giles are color/contrast of the substrate, water type, vegetation, presence of microorganisms, substrate moisture, and texture [16, 27, 28].

The overall complex set of signals that are present in such breeding habitat and are used by *An. gambiae* to locate preferred oviposition site act in two contradictory ways. Whereas such habitats exert a "pulling" effect, unsuitable pools may exert an active "pushing" effect, and it is the integrated "push/pull" effects of these different signals that may effectively guide an insect to a habitat suitable for its species [3]. Previous studies designed to clarify the types of signals that mediate the attraction of *An. gambiae* to specific pools demonstrated mediation of several signals [21, 29]. Volatiles associated with the microbial population in preferred anopheline pools were found to be important initial interspecific attractants [21]. In general, two intraspecific signals were shown to regulate oviposition: a volatile pheromone and a contact deterrent associated with the larval stages of the mosquito [29]. This pair of signals may play an important role in fine-tuning the balance between the exploitation of a suitable breeding site and the avoidance of intra-specific competition and other effects of overcrowding [3, 29–33].

Attractant and repellent compounds for mosquitoes oviposition, including anopheline, have been identified from several sources such as hay infusion [18, 34], water-associated bacteria [21, 35, 36], mosquito oviposition and larvae holding water, pheromones [6, 21, 29, 37], and exudates from aquatic competitors or predators [13, 38]. The different sources of stimuli result in patterns of distribution of immature-stage mosquitoes that reflect differences in the suitability of sites for the development of different species [29, 39]. Understanding this point is not only important for its potential in developing a new strategy, but also important in terms of targeting larval control. Here below are the main sources and substances mediating habitat selection that acts as repellent or attractants to gravid mosquitoes.

2.2. Immature Stages Conspecific. Gravid mosquitoes may be attracted to habitats with conspecific larvae, because presence of conspecific larvae may indicate suitable habitats for the species [21, 40, 41]. Conspecific attraction has been described as a means for females to exploit information collected by other females. Rather than gathering information on a multitude of environmental factors potentially affecting offspring growth, a process constrained by energy, time, and/or sensory capabilities, females may be able to quickly assess habitat suitability by sensing the reproductive success of previous females [42]. Interestingly, conspecific attraction has been observed across numerous animal taxa [26, 43–45], such as birds, mammals, reptiles, fish, and insects, including other mosquitoes [19, 46]. For *Ae. aegypti*, attraction of gravid females to containers with immature conspecifics may seem at first counter-productive [47]. These habitats previously released olfactory cues which have attracted the first gravid mosquito and subsequently the offspring colonised the habitats. Thus it is evident that habitats have potential olfactory cues for more gravid to oviposit with substantial ability to support the larvae developmental needs.

In large laboratory cages, when given choices gravid females of *An. gambiae s.l.*, deposit more eggs in turbid water from natural larval habitats than in clear water [28]. On the other hand, previous studies have shown that habitat water with debris has more larvae and more emerging adults. A plausible reason is that debris is potential food source for the larvae of *An. gambiae s.l.* [48]. In other studies, the number of eggs laid by the female *An. gambiae s.l.* during the peak oviposition time has been demonstrated to be affected by the suitability of the habitat resource types [16, 27, 49]. Both laboratory-reared and wild-caught mosquitoes of *An. gambiae s.l.* have been shown to significantly prefer anopheline habitat water to the culicine habitat water [21]. In two studies involving *An. gambiae s.s.,* Brandon and others demonstrated that, the larval rearing water of the different mosquito strains produced a signal that yielded a positive oviposition response from *An. gambiae s.s.* gravid females of the same region (strain) [14].This not only implies the presence of conspecific attractant but also could be a model for how speciation could arise within related taxa of mosquitoes [14].

Aedes atropalpus is a rock-pool breeder that utilizes the same temporary sites repeatedly in nature. In laboratory experiments, this species preferentially oviposited significantly more eggs in water that had previously held conspecific larvae than in distilled water indicating that the attractive substance was probably a pheromone [50]. The apparent stability and low volatility of the active substance would be advantageous in this habitat; the substance can remain active over long periods and can be reconstituted after the drying and subsequent reflooding of the rock pools. The larvae-produced activity remained both when the larvae were first purged with kaolin and when the water containing larvae was microfiltered. The active substance resulted in greater egg deposition only when the females came in contact with the solution. Thus it was a contact stimulant rather than an attractant [6].

Conspecific reflects a trade-off between the risk of choosing an unsuitable habitat and the cost of intraspecific competition [5, 30, 32]. For example, larval density can affect site selectivity. Rearing water of higher larval density (900 larvae per liter) was repellent to ovipositing *An. atropalpus* females reared under axenic conditions [51]. In a previous study, *An. gambiae s.s.* laid significantly more eggs in containers with low larval density than in containers with higher densities [13]. Probably, this is because those high larval densities negatively influenced several components of anopheline mosquito fitness, including larval survivorship [52], development rate [53], adult lifespan [53], adult size [31, 54], and female fecundity [54–56]. From this standpoint, it would seem advantageous for ovipositing females to view conspecifics as competitors to their own progeny [47].

Such threshold of larval density has been demonstrated with *Ae. aegypti* as well. Laboratory assays have demonstrated a dose-specific oviposition response that increased with conspecific densities up to 1 larva/mL and decreased thereafter [35–37]. *An. gambiae s.s.* laid significantly more eggs in containers with five larvae than in containers with higher densities (more than 50) [13]. It has been suggested that, at least with *Ae. aegypti*, a small portion of female population may act as "founders" [57], choosing noncolonized sites based on environmental indicators of quality, whereas the majority of females respond predominantly to conspecific cues [47]. This could be true with *An. gambiae s.l.* despite the fact that both females have been reported to be using multiple breeding sites for oviposition [58, 59]. This seemed to occur within a distance of few meters and mainly due to increasing the chance of reducing the risk of progeny failing to develop into adult stage [60].

2.3. Vegetation Volatiles. Middle-range volatiles from plants may function as chemical cues for the female's oviposition response in *Anopheles* mosquito species. In general, vegetation as visual cues evidently influenced oviposition on soil or water substrates. For example, while *Anopheles funestus* breeds mainly in marshes and swamps that contain tall grasses, *Anopheles hermsi* increased with increase in the density of aquatic macrophytes (Myriophylluy maquaticum) up to 1,000 stems per m^2 [24, 61]. Some anopheline species generally prefer to lay eggs in habitats associated with vegetation. Given a choice, *Anopheles minimus s.l.* prefer to oviposit their eggs where plants are present compared to sites with bare soil. Small-leaved plants were significantly more attractive to ovipositing female of this species compared to habitats with grasses [62].

Anopheles gambiae Giles *s.l.* has been thought to avoid stagnant water populated with vegetation. This is likely not accurate as the species has been found to deposit eggs in rice fields at all stages of vegetative maturity [63]. Fillinger et al. [64] have strongly challenged the idea that *An. gambiae* avoids habitats with emergent vegetation like grasses. Minakawa et al. [11] provided evidence that *An. gambiae* is commonly found in association with grasses, but it was not clear whether presence of larvae in such habitats results from hatched eggs laid on or around wet grasses, or whether larvae were carried there by flowing water. This question has been addressed in laboratory oviposition choice experiments by Huang et al. [65]. They found that *An. gambiae s.l.* females preferred to lay their eggs on bare wet soil rather than on soil populated with grasses. However, in no-choice experiments, when typical puddles over bare soil are unavailable, *An. gambiae s.l.* has the capacity to oviposit into grassy aquatic habitats and short grasses were more preferred than medium and tall ones [48, 66].

However, some plant species may act as specific attractants more than others. For example, a strong positive association has been found between *An. Albimanus* Wiedemann larval abundance and specific vegetation forms of water containing *Brachiaria mutica*, *Cynodon dactylon*, *Jouveastraminea*, *Fimbristylis spadicea*, and *Ceratophyllum demersum* [38, 67, 68]. This suggested that females of this species may be using cues from these plants to select suitable places to lay their eggs. This has been addressed by an experiment conducted in a wind tunnel and indicated that gravid female of *An. albimanus* response is mediated by chemical cues from these plants. Gas chromatography and mass spectrometry analysis of the organic extracts from these plants showed a mixture of terpenoid and alcohol compounds, among them: guaiacol, phenol, isoeugenol, longifolene, caryophyllene, phenyl ethyl alcohol, and p-cresol [67].

2.4. Moisture Content. Hydration is one of the critical oviposition site selection qualities for *An. gambiae s.l.* [27]. In a previous study, a strong positive correlation was found between moisture content and the degree of egg laying, which peaked at saturation with standing water [27]. It has been indicated that these species prefer flooded soil over dry or moist soil as oviposition substrate under the insectary environment. However, when flooded oviposition substrates were removed, females laid all eggs on moist soil substrates [69]. Besides, anopheline eggs remain viable only on wet substrates [24] and gravid females often choose a moist surface to oviposit their eggs in the laboratory and in the field [16, 65, 70]. In general, *An. gambiae* females are very sensitive to small changes in moisture while choosing an oviposition site [27]. Probably, this is because these eggs cannot tolerate prolonged desiccation, an observation not applicable to some mosquitoes, for example, *Aedes* and *Ochlerotatus* [24]. Survivorship of *An. gambiae s.l.* eggs in drying soils held in a laboratory was found to be inversely related to time after deposition; that is, very few eggs in drying soils hatched after 12–15 days upon reflooding [71]. It has been suggested that the egg stage of *An. gambiae s.l.* might contribute to the short-term survival of this vector during dry periods in natural conditions [71]. This has further been confirmed in laboratory experiment in which high temperature was found to cause egg mortality [16]. This study concluded that moist mud around puddles constitutes suitable habitat for *An. gambiae s.l.* eggs; however, eggs on the surface of dry soil under direct sunlight are unlikely to survive for more than a few hours.

2.5. Predator's Kairomones. There are growing lines of evidence that a number of mosquito species detect some predators via chemical cues, causing them to avoid these predators when choosing an oviposition site [13, 19, 30, 41, 72–81]. In general, chemical cues play an important role in predator prey interactions in aquatic environments [82–85]. Predator-released kairomones may induce morphological changes in prey [80, 81], foraging changes by prey [86], and behavioral responses of gravid prey females via oviposition habitat selection [87]. Several studies have shown that mosquitoes chemically detect and avoid backswimmer species when ovipositing *An. gambiae s.l.* species [30, 74]. Munga et al. [13] demonstrated that cues from backswimmers and tadpoles influenced selection of oviposition site by gravid *An. gambiae s.l.* in cages. These results suggested that gravid mosquitoes avoid habitats containing competitors and predators to reduce the risk of mortality of offspring and this behavior is probably one of the mechanisms causing the heterogeneous distribution of *An. gambiae s.l.* larvae [88].

However, little is known about how malaria vector females detect predator-released kairomones in breeding sites, and no such kairomones have been chemically identified. In general, mosquitoes may detect chemicals from the air when the chemical possesses sufficient volatility or, in the case of low volatility chemicals, by a gustatory mechanism involving direct contact with the water [89]. It has been demonstrated that ovipositing *Culiseta longiareolata* female in study site here was deterred from continuing to the central pool, without any direct contact, when predator-released volatile compound(s) emanated from the surrounding channel [80, 81]. *Notonecta maculata* has already been shown to influence oviposition by three mosquitoes species including *An. gambiae s.l.* [13], and the predator-released kairomone(s) may have the same effects in all three mosquito species. The chemicals which may be common to all backswimmers species [77], but not to other predator groups [90], elicit the response in some mosquitoes. Future studies should focus on determining the specific volatile compound(s) released by predators that reduce malaria vector oviposition, particularly *An. gambiae s.l.,* which may then be used in control efforts [80].

2.6. Microbial Volatiles. Microbial populations in breeding sites produce volatiles that serve as semiochemicals for gravid *An. gambiae*. These signals, in conjunction with other (nonolfactory) chemical and physical cues, may be used by the female to assess the suitability of potential larval habitats in order to maximize the fitness of her offspring. Microbes and their metabolites act as ovipositional attractants and/or stimulants for various species of culicine mosquitoes [22, 23, 91–93]. Microbial metabolites emanating from larval habitats might also positively influence ovipositional site selection by anopheline mosquitoes. Indirect lines of evidence have shown that water microbial condition significantly affected oviposition as a substrate preference of anopheline mosquitoes. Knols et al. [17] reported that *An. gambiae* Giles laid more eggs on nonautoclaved soil or water taken from natural larval habitats than on similar but autoclaved materials, suggesting that killing the microbes by autoclaving eliminated the source of ovipositional attractants. In a laboratory experiment, lake water drawn from Lake Victoria attracted more eggs by *An. gambiae* than did any water or infusion type, including water from puddle habitats supporting larvae that are thought to be ideal larval habitat. The author speculated that algal volatiles [94, 95] might play some role in ovipositional stimulation on this type of water [49]. Blackwell and Johnson [96] observed significant electroantennogram (EAG) responses of *An. gambiae* towards volatile components of water samples from Tanzanian breeding sites. The origin of stimulants in mosquito breeding sites and their mode of action towards gravid females are not fully understood, though it has been suggestively linked to microbial activity [9, 15, 35, 36, 97].

Previous studies have shown that microbial volatiles function as oviposition attractants/stimulants to different mosquito species. Bacteria in larval habitats may serve as a direct source of food for the larvae or as modifiers of organic matter in breeding waters, which may give rise to constituents ingested by larvae as well as volatile organic compounds of the breeding site waters [25, 96, 98–100]. Certain bacterial volatiles have been shown to attract *Cx. fatigans* Coquillet [97], *Ae. aegypti* L. [92], and *Cx. quinquefasciatus* Say [18, 93]. In certain cases, bacterial metabolites [97] were thought to be precursors in the synthesis of the volatile attractants. A lower oviposition response was reported after reduction of the number of bacteria either by sterilization, filtering, or addition of antibiotics to the test water or substrate [21, 35, 36, 91]. Indeed, some studies have reported a direct oviposition response toward bacterial cultures or filtrates [16, 23, 92, 93, 97, 101–103]. The majority of these studies have been performed on *Culex* or *Aedes* mosquitoes. For anopheline mosquitoes, Sumba et al. [21] observed an indirect effect of bacteria on oviposition response of *Anopheles gambiae* Giles by comparing soil and water from natural habitats with the same substrate that had been sterilized. The mosquitoes laid significantly more eggs on the nonsterile substrates [21]. Material from larval habitats of *Anopheles albimanus* Wiedemann and *Anopheles vestitipennis* Dyar and Knab (consisting of macrophytes, cyanobacteria, diatoms, and bacteria), when extracted by freeze-drying and presented to gravid females at low concentrations, increased oviposition by females of both species [100]. Direct evidence has found that emissions from a bacterial flora isolated from a larval habitat of *An. gambiae* received significantly fewer eggs than controls, indicating that these emissions under the unnatural conditions were repellent rather than attractive to the gravid females [16, 65, 104]. This bacterial flora included mixtures of bacterial colonies of *Pseudomonas* strains (78%), *Stenotrophomonas*, *Enterobacter*, *Pantoea*, *Klebsiella*, *Acinetobacter*, *Aeromonas*, and *Bacillus* or a lawn of colonies of a field isolate of *S. maltophilia*. Oviposition was neither reduced nor enhanced when field isolates of *Pseudomonas putida* or *Pseudomonas alcaligenes* colonies were presented in the habitat. These results suggest that gravid *An. gambiae* females are sensitive to bacteria-derived odors emanating, as has been suggested for host-seeking females [15], from cultured bacteria from natural larval habitats and that some bacterial odors may be repellent [16]. Recently, 13 putative oviposition attractants for *An. gambiae* mosquitoes were identified from six bacteria, previously isolated from *Anopheles gambiae s.l.* (Diptera: Culicidae) midguts or oviposition sites, subjected to principal component analysis (PCA) based on the relative amounts of volatiles emitted and among these putative, the 3-methyl-1-butanol has been found to be a strong candidate [105]. Further research is needed to confirm these observations. If any of the suggested compounds is confirmed as oviposition attractants, they may be used in traps to monitor or in combination with larvicides to control *An. gambiae* populations.

Bond et al. [106] provided direct evidence for attraction of gravid *Anopheles pseudopunctipennis* Theobald to substrates containing filamentous algae. Torres-Estrada et al. [68] investigated the attraction of *An. pseudopunctipennis* gravid females to oviposition substrates containing *Spirogyra majuscula* algae under laboratory conditions. This experiment has been done based on the well-documented association of filamentous algae with larval abundance [26]. The authors found that gravid females deposited significantly more eggs in cups containing natural algae in water from breeding sites than in cups containing artificial (nylon rope) life-like algae in water from the corresponding natural breeding site or in cups containing natural algae in distilled water. Results from bioassays carried out in the same study with *Spirogyra majuscula* organic extracts indicated that these extracts at concentrations of 0.1%, 0.01%, and 0.001% attracted more oviposition, but concentrations of 1%, 10%, and 100% were repellent. Gas chromatography and mass spectrometry analysis of algal organic extracts revealed a mixture of ethyl acetate and hydrocarbons compounds. These results suggested that the attraction of gravid *An. pseudopunctipennis* to natural breeding sites containing filamentous algae is probably mediated by organic volatiles released by the algae [26].

3. Conclusion

Chemical volatiles influence oviposition site selection as attractants or stimulants. Control tools could be therefore designed to capitalize on the attractant or stimulant properties of semiochemicals influencing malaria vectors oviposition responses in the field. The isolation of determinants for oviposition behaviors in anopheline mosquitoes still remained elusive. Efforts for isolating anopheline oviposition pheromones level have been unsuccessful, probably due to small quantity produced by the immature stages making the study of their structure and function more difficult. This review suggests early investigations which indicates the potential of plant, algae, or bacteria-derived oviposition attractants and stimulants, which could be used to lure females mosquitoes to lethal ovitraps to increase their exposure to insecticide-impregnated substrates [68, 105].

Conflict of Interests

The authors declare that they have no conflict of interests.

Authors' Contribution

Yousif E. Himeidan identified the idea and drafted and wrote up the paper, and Eliningaya J. Kweka, Emmanuel A. Temu, El Amin El Rayah, and Stephen Munga drafted and reviewed the paper. All authors read and approved the final paper.

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