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ORIGINAL PAPER

Olfaction in Asian tiger mosquito *Aedes albopictus*: flight orientation response to certain saturated carboxylic acids in human skin emanations

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Abstract The flight orientation response of nonblood-fed and hungry *Aedes albopictus* females was studied in a Y-tube olfactometer at 10^{-6} to 10^{-2} g odor plumes of saturated carboxylic acids (C_1–C_{20}), in which C_2–C_{18} were the main constituents of human skin emanations. Thirteen acids viz C_1, C_2, C_3, C_5, C_6, C_8 C_9, C_{10}, C_{12}, C_{14}, C_{16}, C_{18}, and C_{20} showed attractance at odor plumes ranging from 10^{-5} to 10^{-3} g doses, while five acids viz C_4, C_7, C_{11}, C_{15}, and C_{19} showed repellence at 10^{-4} to 10^{-2} g to test mosquitoes. Tridecanoic acid (C_{13}) showed attractance only at 10^{-4} g dose while higher doses caused repellence. Dose-dependent reversal of orientation behavior from attractance to repellence was observed at 10^{-2} g plumes of C_5, C_9, C_{10}, C_{13}, C_{17}, C_{19}, and C_{20} acids. The outcome of the study will help in the identification of odoriferous acids as potential attractants, repellents, or attraction inhibitors, which may find their application in the repellent formulations and odor-baited traps for surveillance and control of mosquitoes.

Keywords *Aedes albopictus* · Human skin emanations · Attractant · Repellent · Host-seeking behavior · Olfaction

Introduction

The Asian tiger mosquito, *Aedes albopictus* (Skuse) (Culicidae: Diptera) is a day-biting mosquito, is highly anthropophilic, and resides in urban and suburban areas covered with vegetation. These mosquitoes closely interact with human beings for blood feeding. *Aedes albopictus* has emerged as a potential vector for both dengue and chikungunya viruses and has posed a serious threat to the human community in India and South-East Asian countries. These mosquitoes cause biting annoyance and discomfort to human beings throughout the world, and the problems become much more severe as they also act as vectors of pathogens that cause West Nile virus, yellow fever virus, St. Louis encephalitis, dengue fever, and chikungunya fever (Hochedez et al. 2006). In the recent years, the incidence of dengue and chikungunya has increased dramatically in tropical countries.

Mosquitoes can discriminate different animals due to their ability to recognize host-specific odors for blood feeding (Qiu et al. 2004; Schreck et al. 1981). An enormous attention has been paid to mosquito attractants and repellents as alternatives to pesticides by the researchers around the world in managing mosquitoes, in which many synthetic and natural volatile organic compounds possess the ability to either attract or repel adult mosquitoes (Fradin and Day 2002). The effectiveness of various attractants and other volatile organic compounds that may serve as spatial repellents has been tested extensively against *Aedes aegypti* (L.) mosquitoes (Bernier et al. 2003; Geier et al. 1996; Kline et al. 2003) to protect humans from mosquito biting.

It has been reported that human sweat and human skin residues are highly attractive to *A. aegypti*, *Anopheles gambiae* Giles, and *Culex quinquefasciatus* Say mosquitoes (Acree et al. 1968; Bosch et al. 2000; Braks and Takken 1999; Logan et al. 2008; Puri et al. 2006). A number of host skin emanation chemicals like 1-octen-3-ol, acetone, short-chain carboxylic acids, ammonia, and L-lactic acid have been found to be attractive to *A. aegypti* (Bosch et al. 2000; Geier and Boeckh 1999; Schreck et al. 1981). Several studies have

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demonstrated that ammonia, lactic acid and many carboxylic acids (Bernier et al. 2000; Bosch et al. 2000; Cork and Park 1996; Eiras and Jepson 1991; Smallegange et al. 2005, 2009), acetone, and dimethyl sulfide (Bernier et al. 2007) act as a potential attractant for *Aedes* and *Anopheles* mosquitoes.

Attractant chemicals from host skin emanations appear to provide the most immediate promise for use in traps. Nowadays, researchers are more focused on eco-friendly approaches using semiochemicals (pheromones or parapheromones) of natural and synthetic origin with multiple strategies to control hematophagous insects (Seenivasagan and Vijayaraghavan, 2010; Seenivasagan et al. 2013; 2012; 2010; 2009a; 2009b) exploiting oviposition and flight orientation behaviors. However, effective use of attractants for mosquito control requires an understanding of the mechanisms that attract mosquitoes to humans and animals. Scientific works on the use of human skin emanations to attract *A. albopictus* (Hao et al. 2012; Wang et al. 2006) mosquitoes are scarce. In this research paper, we report hereunder, the flight orientation response of *A. albopictus* females to a series of carboxylic acids (C_1–C_{20}) at various concentrations for the identification of odoriferous acids as potential attractants, repellents, or attraction inhibitors, which could be used as repellents as well as in odor-baited traps for the surveillance and control of mosquitoes.

Methods and materials

Insects

The test mosquito, *A. albopictus*, used in the present study was taken from the laboratory colony maintained in our insectary at 27±2 °C, 70±5 % RH and L10:D14 regime. Test females were kept in wooden cages (750×600×600 mm) with a sleeve opening on one side (Sharma et al. 2008), with sucrose (10 %) solution being offered *ad libitum* to the females. However, they did not have the access to blood meal until the beginning of experiments.

Chemicals

All the carboxylic acids used in this study viz, formic acid (C_1) to arachidic acid (C_{20}) were procured from Sigma-Aldrich/Fluka (Table 1). A stock solution (10 %) of each acid was prepared in HPLC-grade hexane (Merck) by adding the required amount (volume/weight) to the solvent. According to the purity of the chemicals, volume/weight was adjusted to prepare the stock solutions. For each chemical, five concentrations (0.0001, 0.001, 0.01, 0.1, and 1 %) were prepared by serial dilution and stored in deep freezer.

Y-tube olfactometer

Flight orientation of *A. albopictus* females was studied using Y-tube olfactometer as previously described by Seenivasagan et al. (2009a), with a modification that the mosquitoes used in these experiments were 5–7-day-old nonblood-fed and hungry host-seeking females. In each replicate, a set of 20 hungry female mosquitoes, which readily oriented to human hand, were aspirated out from the cage and used in the experiments. Seven replicates were performed for each concentration of the carboxylic acids. Before stimulation, the mosquitoes were given 5-min time to acclimatize in the release chamber. Between the replicates, a constant stream of fresh air was purged into the olfactometer. Orientation experiments in dual-choice conditions were performed, in which precisely 200 μl of the test chemicals at various concentrations was applied onto a piece of filter paper and then loaded onto an odor cartridge after evaporation of the solvent. The air flow was maintained at 50 l/min during the experiment. Between replicates the positions of test stimuli were alternated. The bioassay was conducted for 3 min until all the mosquitoes fled from the releasing chamber and entered into the upwind end of the olfactometer. The olfactometer was cleaned thoroughly after testing each of the chemicals. The number of mosquitoes that entered into treatment and control chambers in a replicate was considered for analysis.

Statistical analysis

Data of flight orientation response in a Y-tube olfactometer were converted to orientation index, by the formula Orientation Index = (Nt − Nc)/(Nt + Nc), where Nt is the number of mosquitoes caught in the treatment chamber and Nc is the number of mosquitoes caught in the control chamber, and subjected to two-way analysis of variance (Table 2) using SigmaStat v2.03 (SPSS Inc, Chicago, IL).The differences between the treatment means were separated by least significant difference (LSD), and *p* value <0.05 was considered statistically significant among the test chemicals.

Results

Orientation index values of different carboxylic acids apparently demonstrated the flight choice of *A. albopictus* females to the test odor plumes over control stimulus in terms of both attractant and repellent effects. Carboxylic acids with carbon atom atom C_1, C_2, C_3, C_5, C_6, C_8, C_9, C_{10}, C_{12}, C_{14}, C_{16}, C_{18}, and C_{20} were attractive to *A. albopictus* females. The odor plumes of C_4, C_7, C_{11}, C_{15}, C_{17}, and C_{19} acids repelled the host-seeking females. Dose-dependent increase in orientation response was observed for formic, pentanoic, nonanoic, decanoic, dodecanoic, and stearic acids. At the highest dose (10^{-2} g), *A. albopictus* females exhibited a reversal in the

Table 1 Carboxylic acids used in the flight orientation experiments against *Aedes albopictus* females

CAS number	Carboxylic acids	Purity (%)	Molecular weight (g/mol)	Source
64-18-6	Formic acid[a]	98	46.03	Fluka
64-19-7	Acetic acid	98	60.05	Fuka
79-09-4	Propanoic acid	99.5	74.08	Fluka
107-92-6	Butanoic acid	99	88.11	Aldrich
109-52-4	Pentanoic/valeric acid	>99	102.13	Aldrich
142-62-1	Hexanoic acid	>99.5	116.16	Fluka
111-14-8	Heptanoic acid	99	130.19	Aldrich
124-07-2	Octanoic acid	99.5	144.21	Fluka
112-05-0	Nonanoic acid	>96	158.24	Fluka
334-48-5	Decanoic acid	>98	172.26	Fluka
112-37-8	Undecanoic acid	>97	186.29	Fluka
143-07-7	Dodecanoic acid	>98	200.32	Fluka
638-53-9	Tridecanoic acid	>99	214.34	Fluka
544-63-8	Tetradecanoic/myristic acid	99.5	228.37	Fluka
1002-84-2	Pentadecanoic acid	>99	242.40	Fluka
57-10-3	Hexadecanoic/palmitic acid	>99	256.42	Fluka
506-12-7	Heptadecanoic acid	>98	270.45	Sigma
57-11-4	Octadecanoic/stearic acid	>98.5	284.48	Fluka
646-30-0	Nonadecanoic acid[a]	>98	298.50	Fluka
506-30-9	Eicosanoic/arachidic acid[a]	>98	312.53	Fluka

[a] Not reported in human skin emanations (Bernier et al. 2000)

orientation from attractance to repellence for pentanoic, nonanoic, decanoic, tridecanoic, heptadecanoic, and eicosanoic acids. Similarly, hexanoic acid which did not elicit any significant attractance at lower doses (10^{-6}g to 10^{-4}g); attracted 20 % and 30 % of *A. albopictus* females respectively at 10^{-3}g and 10^{-2}g odor plume.

Females of *A. albopictus* displayed a characteristic orientation behavior demonstrating the behavioral threshold by dose-dependent reversal of their orientation to tridecanoic acid (C_{13}) in which the odor plume (10^{-6} and 10^{-5} g) at lower doses did not elicit any significant response, while 10^{-4} g plume attracted the females. In contrast, 10^{-3} and 10^{-2} g plumes repelled the females. Similarly, heptadecanoic acid (C_{17}) at 10^{-6} g attracted the females while all other doses turned repulsive to *A. albopictus* females (Fig. 1). Eicosanoic acid showed attractance at 10^{-5} to 10^{-3} g plumes, however, repelled the mosquitoes at the highest dose. Repellent effect of few carboxylic acids viz butanoic, heptanoic, undecanoic, and pentadecanoic acids increased in dose-dependent manner as the negative orientation index increased with increasing doses. Undecanoic and nonadecanoic acids at higher doses exerted a consistent repellency to test mosquitoes, as evidenced by a slight increase in mosquito orientation to control chamber.

Discussion

Laboratory studies aimed at elucidating the volatiles from human skin emanations that mosquitoes utilize for host location have yielded several active mixtures and individual substances, having carboxylic acids as an important component of human sweat (Cork and Park 1996). In subsequent studies, volatile organic compounds (VOCs) emerging from sweat, breath, and other emanations of hosts constituting a complex mixture of volatiles including short- and long-chain

Table 2 Results of the two-way analysis of variance on the orientation indices exhibited by *Aedes albopictus* females to carboxylic acid odors in the Y-tube olfactometer

Source of variation	DF	SS	MS	F	P
Total	699	60.258	0.086		
Carboxylic acids	19	32.401	1.705	80.344	<0.001
Concentration	4	1.0260	0.256	12.082	<0.001
Carboxylic acids × Concentration	76	14.096	0.185	8.738	<0.001
Residual	600	12.735	0.021		

DF Degrees of Freedom, *SS* Sum of Squares, *MS* Mean Squares, *F* F-test, *P* *P*-value

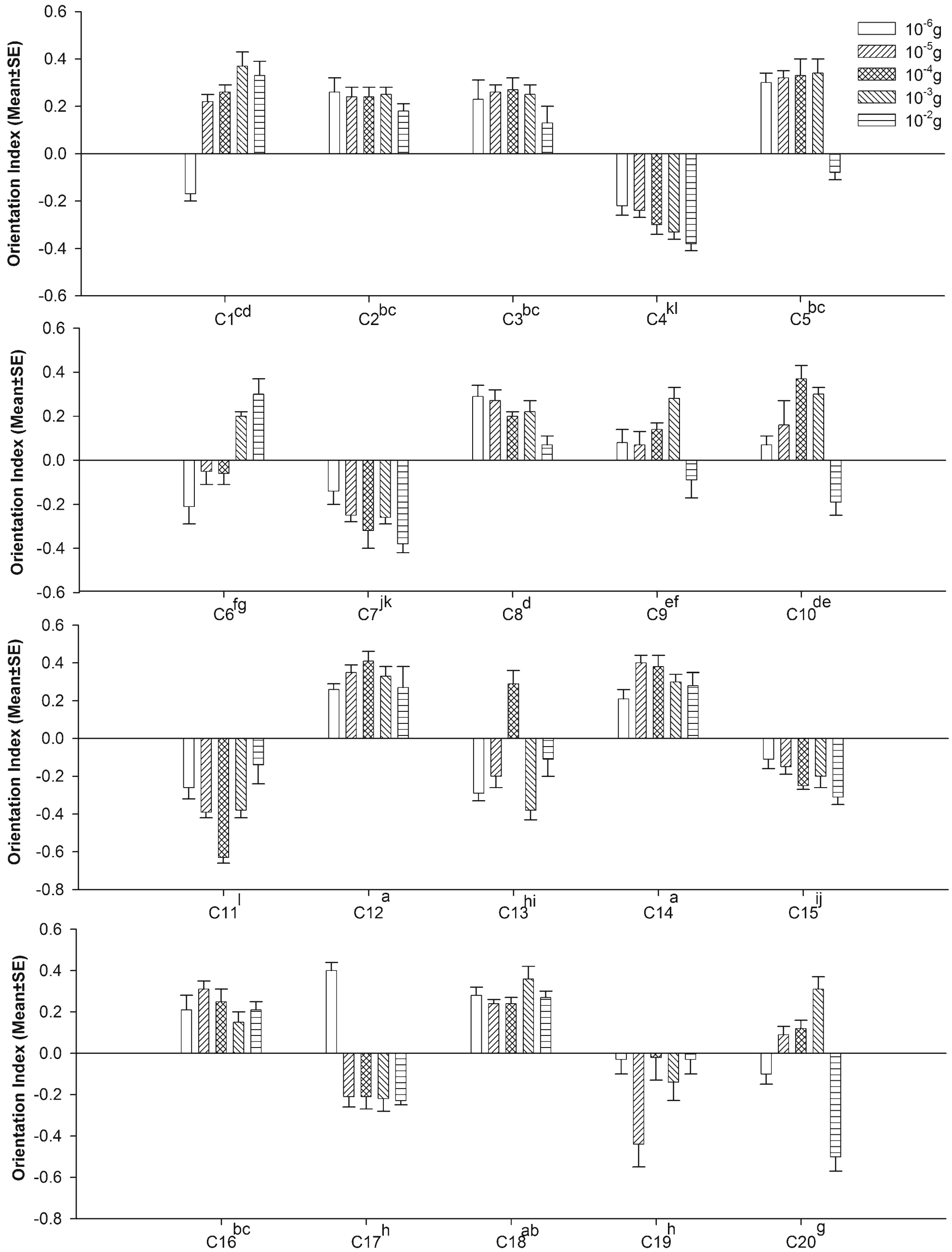

Fig. 1 Flight orientation response of *Aedes albopictus* females to various concentrations of carboxylic acids (C_1–C_{20}, Table 1). Carboxylic acid legends with different *alphabet superscripts* are significantly different (two-way ANOVA, $P<0.001$, Table 2)

hydrocarbons, alcohols, carboxylic acids, ketones, and aldehydes have been identified (Bernier et al. 2000; Braks et al. 2001; Curran et al. 2005; Gallagher et al. 2008; Penn et al. 2007). In earlier studies, mostly C_3–C_{18} acids have been evaluated, and they were found to be attractive to *A. aegypti* (Bosch et al. 2000), *A. gambiae* s.s. (Smallegange et al. 2005), and *C. quinquefasciatus* (Puri et al. 2006).

Response of *A. albopictus* females to a series of carboxylic acids (C_1–C_{20}) has not been previously reported. In the Y-tube olfactometers, *A. albopictus* females were exposed to concentrated kairomone plumes in confined spaces, less than 2 m from the odor source, facilitating odor-mediated upwind flight that confirms the attractive, repulsive, or inhibitory nature of test odor plumes. In this study, carboxylic acids viz C_1–C_3, C_5, C_6, C_8–C_{10}, C_{12}, C_{14}, C_{16}, C_{18}, and C_{20} were attractive, while C_4, C_7, C_{11}, C_{15}, and C_{19} repelled *A. albopictus* females. Puri (2003) has found that C_3, C_6–C_{13}, and C_{17} plumes were attractive to *A. aegypti* at 500 µl of 10 ppm of respective acids loaded in an olfactometer, while C_{14}–C_{16} and C_{18} repelled the females at the same dose. In case of *C. quinquefasciatus*, C_3, C_6–C_{11}, C_{13}–C_{14} elicited increased orientation, while C_{15}–C_{18} reduced flight orientation response at 10 ppm (Puri 2003). In contrast, *Anopheles stephensi* Liston females were repelled by C_{10}, C_{11}, C_{16}, and C_{17} plumes, while other acids showed attractance (Puri 2003). Till date, nonadecanoic and eicosanoic acids have not been reported as components of human sweat. Yet, eicosanoic acid presented a clear case of insect behavioral threshold, wherein at 10^{-6} g, no attraction was observed; at 10^{-5} to 10^{-3} g, attraction was observed; and at 10^{-2} g, repulsion of mosquitoes was observed, indicating that optimum concentration of a volatile elicits significant behavioral response. In contrast, C_{19} showed varying levels of repellency to *A. albopictus* at all concentrations tested.

Bosch et al. (2000) have reported that the addition of C_1–C_3, C_5–C_8, and C_{18} to lactic acid attracted the females of *A. aegypti*, while the addition of C_9, C_{11}, and C_{14} reduced their attraction. In contrast, C_3, C_4, 3mC_4 (3-methyl-butanoic), C_5, C_7, C_8, and C_{14} acids when added to ammonia + lactic acid blend resulted in an increase in the number of *A. gambiae* females flying into the olfactometer at one or more of the tested concentrations (Smallegange et al. 2009). In our experiments, butanoic, heptanoic, and pentadecanoic acids repelled *A. albopictus* females at all tested concentrations. Undecanoic acid (C_{11}) repelled 63 % of the female *Aedes albopictus* at 10^{-4} g, and further increase in concentration resulted in reduced orientation, possibly due to the saturation of olfactory receptors present in the antennal sensilla (Seenivasagan et al. 2009b) of *A. albopictus* mosquitoes. Ali et al. (2012) have reported that octanoic, decanoic, undecanoic, dodecanoic, and tridecanoic acids repelled *A. aegypti* mosquitoes at 25 nmol/cm^2 concentration, displaying >0.80 biting deterrence index (BDI). Tetradecanoic acid was attractive over a range of concentrations to *A. aegypti* and *A. stephensi* (Puri 2003), *A. gambiae* (Smallegange et al. 2009), and *C. quinquefasciatus* (Puri et al. 2006). Although C_{14} was attractive to *A. albopictus* females in our experiments, a slight decline in the orientation was observed at 10^{-3} and 10^{-2} g plumes; however, a significant repellence at 10^{-5}g plume was observed against *A. aegypti* females (Puri 2003).

Our results suggest that only a few of these carboxylic acids, depending on their chain length and concentration, contributed to the orientation of *A. albopictus* to human skin emanations. This study also demonstrated that aliphatic acids can act in both ways (attractant/repellent) depending on their concentration and molecular structure. Further pieces of evidence have emerged based on the dose-dependent reversal in the orientation behavior of female mosquitoes to C_5, C_9, and C_{10} at 10^{-2} g plume, tridecanoic acid (C_{13}) at 10^{-3} and 10^{-2} g, and heptadecanoic acid (C_{17}) at 10^{-5} to 10^{-2} g wherein the lower doses of these acids were slightly attractive to the test insects. Different mosquito species may not possess a similar host odor preference, and there cannot be a single lure for all mosquitoes, which can be exploited for use in traps. Our results combined with the previous findings of various research groups suggest that further research is required to develop an optimum lure for diurnally active *A. albopictus* mosquitoes and its evaluation under laboratory, semi field, and field conditions for successful integrated vector management programs.

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