Environ Sci Pollut Res
DOI 10.1007/s11356-017-9624-y

RESEARCH ARTICLE

Anti-oviposition activities of used sock media against a dengue vector: prospects of eco-friendly control and solutions to pollution

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Received: 23 October 2016 / Accepted: 26 June 2017

Abstract Yearly, huge amounts of sock refuse are discarded into the environment. Socks contain many molecules, and worn ones, which are rich in smell-causing bacteria, have a strong influence on animals' behaviors. But the impacts of sock odor on the oviposition behavior of dengue vectors are unknown. We assessed whether *Aedes albopictus* changes its oviposition activity in response to the presence of used socks extract (USEx) in potential breeding grounds, using choice and no-choice bioassays (NCB). When furnished even chances to oviposit in two sites holding USEx and two others containing water (control), *Ae. albopictus* deposited significantly less eggs in USEx than in water sites. A similar pattern of oviposition preference was also observed when there were more oviposition options in water. When there were greater oviposition opportunities in USEx sites, *Ae. albopictus* oviposited preferentially in water. Females laid significantly more eggs during the NCB involving water than USEx. Also, significantly more mature eggs were retained by females in the NCB with USEx than in that with water. These observations strongly suggest the presence of molecules with either repellent or deterrent activities against *Ae. albopictus* females and provide an impetus to advocate the integration of used socks in dengue control programs. Such applications could be a realistic end-of-life recourse to reroute this waste from landfills.

Keywords Sock waste · Dengue vector · Oviposition repellence · Egg retention

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Introduction

Dengue viruses are still a continuous public health threat worldwide (Messina et al. 2013; Fares et al. 2015). Previously thought of as the main flavivirus transmitted by female *Aedes* mosquitoes, these viruses have been surpassed by Zika virus in many dengue endemic areas (Hennessey et al. 2016), causing a public health emergency of international concern (WHO 2016). Chemical insecticides—the principal strategy against dengue vectors (WHO/WPR 2010)—have become ineffective due to the development of resistance among mosquito populations (Whalon et al. 2008; Wilke and Marrelli 2015) and the narrowing spectrum of effective agents (Dusfour et al. 2010). Therefore, it is becoming increasingly necessary to search for alternative vector control strategies.

Published online: 25 July 2017

In general, for disease transmission and population maintenance to occur, a female mosquito must take a blood meal from a susceptible host and lay eggs. As mosquitoes depend largely on blood meals and oviposition for population maintenance, these aspects of mosquito biology should receive the greatest attention when seeking new control strategies. Host seeking and location by female mosquitoes are mediated by host-derived physical and chemical cues (Verhulst et al. 2011). Volatile agents released from human skin provide essential cues that guide mosquito females to their host (Cardé and Gibson 2010). Skin bacteria play an important role in the production of human body odor, and without bacteria, human sweat is odorless (Shelley et al. 1953). Among dengue vectors, semiochemical cues are used by gravid females to select an oviposition site (Allan and Kline 1995). These include volatile stimulants/deterrents together with contact and attractants/repellents, which most often originate from fermenting or decaying organic materials (Millar et al. 1982; Ikeshoji et al. 1975) or bacteria and/or their metabolites (Trexler et al. 2003; Ikeshoji et al. 1975). The human skin microflora is an underlying cause of variations in human attractiveness for malaria vectors (Verhulst et al. 2011). *Anopheles gambiae* mosquitoes preferentially bite the foot region of humans (DeJong and Knols 1995) and have been shown to respond positively to Limburger cheese (Knols et al. 1997). The cheese gets its aroma from *Brevibacterium linens*, which is a close relative of *Brevibacterium epidermis*, a dermal bacterium involved in foot odor production (Braks et al. 2000). Dengue mosquito females repeatedly attempt to bite around the feet and ankles (Shirai et al. 2002), regions that are usually covered with footwear worldwide.

Worldwide footwear use has doubled every 20 years (Staikos 2006). This includes socks, a basic commodity of which the demand has been increasing gradually over the last few decades. For example, in the UK, the demand for socks is projected to reach 1.35 million dozen pairs and 1.72 million dozen pairs by 2017 and 2022, respectively (Ethio Embassy UK 2016). As a result, the amount of sock refuse will increase in the coming decade. Socks are made from a variety of materials including cotton, wool, nylon, acrylic, polyester, olefins, polypropylene, silk, bamboo, linen, and cashmere (Abd El-Hady 2014). Many sock models incorporate silver nanoparticles (Benn and Westerhoff 2008) and copper (Abd El-Hady 2014). When used socks are discarded, they can be carried as runoff by storm water to aquatic habitats where toxic chemicals will leach out and cause serious impacts on the fauna. Submission of polyester in water leaches out succinic acid, adipic acid, mandelic acid, terephthalic acid, 1,4-butanediol, ethylene glycol, styrene glycol, and 1,4-cyclohexane dimethanol that are toxic to plants and animals (Kim et al. 2001). Polyester is made of thermoplastics (Rosato et al. 2004), which contribute to microplastics pollution (Napper and Thompson 2016). Microplastics have been reported ingestible by fish and other aquatic animals (Hall et al. 2015), leading to serious bleach and stress that may result in death (Hopley 2010). Polyester, nylon (Vogler 2013), and acrylic fibers contribute to microplastics pollution (Napper and Thompson 2016). Microplastics consumed by fish can also move up the food chain and deliver chemical contaminants (Browne et al. 2011, 2013).

Socks are protective knitwear for the foot, which is among the body's greatest producer of sweat (Abd El-Hady 2014). The key role of the material components of the sock is to absorb perspiration (Eng 2010) while providing anti-injury, antifrictional, and antibacterial functions (Abd El-Hady 2014). Sweat creates a beneficial environment for bacteria to grow and produce foul-smelling substances (Kanda et al. 1990; Kanlayavattanakul and Lourith 2011). When worn along with shoes, socks increase the surface area in which the bacteria can thrive. Brevibacteria are considered a major cause of foot odor (Sharquie et al. 2013) via ingestion of dead skin from the feet and conversion of methionine into methanethiol, which has a putrid smell (Smith 2006). Propionibacteria produce propionic acid by breaking down amino acids (Woskow 1991), releasing a vinegar-like odor (Pommerville 2016). *Staphylococcus epidermidis* degrades leucine present in sweat into isovaleric acid, which gives a strong cheesy odor (Ara et al. 2006).

Although odorous socks are repellent to most humans, there are attractive to many animals (Smith 2006; Lindsay 2001). Sock odor also has a strong influence on the behaviors of animals, including insects. For example, hanging smelly socks around a home has been reported to repel deer (Maureen 2001) and to be attractive to dogs (Lindsay 2001) or bears (Smith 2006). The scent from socks worn for 12 h has been reported to be enticing for mosquito-eating spiders (Cross and Jackson 2011). The jumping spider has been reported to prey upon mosquitoes that have fed upon blood. It is attracted to the same smell for this reason, and this has been demonstrated using an olfactometer loaded alternately with clean and smelly socks (Gill 2011). There have been some research efforts into testing the effects of foot odor against mosquito vectors. Malaria mosquitoes were reported to be attracted to foot regions (DeJong and Knols 1995) and volatiles reminiscent of human foot odor (Knols et al. 1997; Lacey and Cardé 2011). Traps baited with human foot scent collected via socks were reported to be more highly attractive to host-seeking females of *Anopheles gambiae* than carbon dioxide (Okumu et al. 2010; Njiru et al. 2006). Washed feet have been documented to be not enticing for blood-seeking mosquito females (DeJong and Knols 1995; Knols 1996). These attributes of the feet and worn sock odors in manipulating the behaviors of mosquito vectors have been explored as a conceptual framework for generating trap devices (Njiru et al. 2006; Okumu et al. 2010). Most of these studies were performed on host-seeking females of *Anopheles* and *Culex* and did not involve gravid females. There is evidence that dengue mosquito females tend to prefer biting the foot and ankle regions of human hosts (Shirai et al. 2002). Some scientists

tested ecologically/behaviorally effects restricted on host-seeking females on gravid ones (Tikar et al. 2014; Afify et al. 2014). However, the effects of foot odor or smelly socks on dengue vectors' oviposition remain largely unknown. This study was performed to assess the behavioral effects of used socks on *Aedes albopictus*. We examined whether gravid females modify their oviposition responses and behavior with regard to the presence of different levels of competition between oviposition sites with used socks extract (USEx) and water.

Materials and methods

Mosquito source

A Borneo strain of *Ae. albopictus* kept under controlled conditions (21–34 °C, 60–86% relative humidity, and photoperiod 13:10 h light:dark, with 1 h of dusk) at the Entomology Unit (External Laboratories of the Faculty of Resource Science and Technology (Universiti Malaysia Sarawak, Kota Samarahan, Malaysia) was used for this study. Routinely, 4–5-day-old females maintained on sugar solution with males were blood-fed on hamsters for 30 min (Approval from Biological Research Ethics Committee at University Malaysia Sarawak). Three days after blood feeding, eggs were collected in oviposition vials (250-mL plastic containers interiorly equipped with filter papers) containing 30 mL of tap water. Eggs were kept as a stock colony adopting the method reported elsewhere (Dieng et al. 2013a). Samples of eggs dried under laboratory conditions were hatched in tap water and five replicates each with 500 first-instar larvae were placed in plastic trays (4-L capacity; As One Corporation, Osaka, Japan) holding 800 mL of water. Larvae were fed 0.15 g of powdered cat food pellets (ProDiet Cat Food, Malaysia) every 48 h, and the water medium was replaced once during larval development. Pupae were collected in 250-mL plastic vials containing 15 mL of water and transferred into mosquito cages (30 × 30 × 30 cm, BugDorm; MegaView Science Co., Ltd., Taiwan). Adults were continuously provided with 10% sugar solution.

Experimental females

To produce experimental adults, egg samples from the colony stock were flooded in tap water and four larval population replicates each with 200 newly hatched larvae were reared as outlined above. Adults were kept on a 10% sugar solution and females were offered blood meals for 30 min from immobilized hamsters 3–4 days postemergence. Fully engorged females that were allowed to digest their meals for 3 days were used for oviposition bioassays. They were referred to as gravid females (GFs).

Experimental features

All bioassays were carried out adopting the experimental design published elsewhere (Satho et al. 2015) with slight modifications. The oviposition site unit was made of a square of polystyrene (side length = 25 cm) and four acrylic containers (depth = 7.3 cm, diameter = 3.3 cm). Each cup was equipped with a section of filter (length = 8 cm, width = 8 cm) that covered the entire interior of the container and acted as an egg deposition substrate. The four containers were placed in holes made in each of the corners of the polystyrene. To avoid any potential position bias, the arrangement of containers was changed from one replicate to another as described elsewhere (Dieng et al. 2014). In this clockwise replication strategy, a replicate corresponded to one arrangement of the four containers on the square. The green arrows indicate the course of shift in position of the oviposition containers. For each bioassay replicate, a new group of 10 GFs and fresh oviposition media were used. A vial holding a 10% sugar suspension was attached at the upper center of the cage to feed GFs during the bioassay (Fig. 1). In all bioassays, females were allowed to oviposit for a period of 7 days.

Experimental socks and extracts

White men's low-crew nylon socks (polyamide 90%, acrylic and spandex 10%) similar in composition to those used by Matowo et al. (2013) were used in this study. This type of sock increases the amount of sweat (EPodiatry.com 2016) and is effective in accumulating and preserving foot odor (Njiru et al. 2006). For each experiment, new socks were worn with shoes for 12 h (6 h on day 1 and 6 h the next day, with socks kept inside the shoes between the two wearing periods) by the same person. We considered a sock worn for this period as a used sock. Water extraction was carried out according to recently published procedures for tea (Dieng et al. 2016). A pair of freshly worn socks was cut into pieces and weighed (Vibra analytical balance; Shinko Denshi Co. Ltd., Tokyo, Japan). An amount of 0.50 g of sock slices was submerged in 400 mL of tap water and allowed to seep. After 1 h of immersion, the infusion was filtered through a piece of fine-mesh mosquito net. The resulting solution tagged as used socks' extract (USEx) was utilized immediately for oviposition bioassays.

Egg deposition responses to sock extract and water environments

To examine whether the oviposition of *Ae. albopictus* is influenced by USEx, females were given equal chances to oviposit in USEx and water. Ten 4–5-day-old GFs and two 4–5-day-old males (2–5 days old) were placed in a mosquito cage (30 × 30 × 30 cm) with an oviposition unit. Two containers were

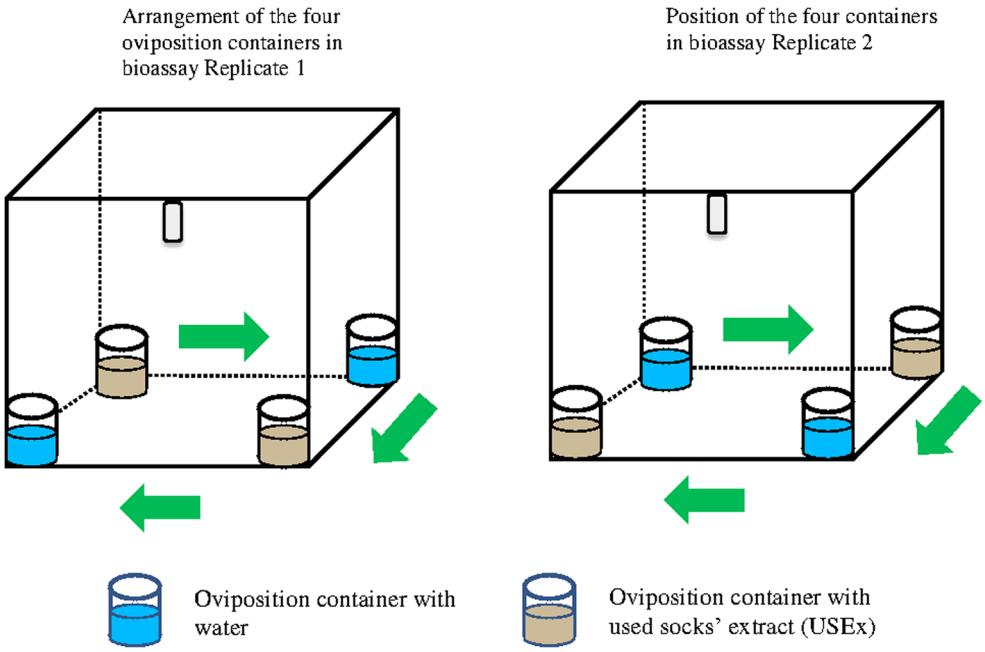

Fig. 1 Oviposition choice bioassay design: the oviposition containers were held by the square polystyrene placed at the bottom side of the mosquito cage; a bioassay replicate coincided with one arrangement of the four containers on the square; the *green arrows* show the route of switching of the arrangements of the containers

each filled with 30 mL of USEx and the same volume of water was added to the two other containers (control). Two bioassays, each with four replicates (eight cage replicates), were run.

To determine how USEx affects the oviposition choice of *Ae. albopictus* when egg deposition chances are biased toward water, *Ae. albopictus* females were offered a choice between USEx and water containers, but with different representativeness. Ten GFs were encaged and provided with the following egg deposition sites: (i) water container 1, (ii) water container 2, (iii) water container 3, and (iv) container with USEx. Four cage replicates were run.

To assess how USEx influences the oviposition site selection of *Ae. albopictus* when there are greater options to lay eggs in USEx containers, the same number of GFs, cage replicates, and experimental design as described above for experiment 2 were also set up and run. Here, however, the ten GFs were given the following four conditions for egg deposition: (i) USEx container 1, (ii) USEx container 2, (iii) USEx container 3, and (iv) water container.

Oviposition rate and egg retention activity to used sock medium

To examine the levels of oviposition responses of *Ae. albopictus* with regard to the type of egg deposition site, two bioassays were performed in quadruplicate as described in experiment 3, but with some modifications: in the first bioassay, the ten GFs were provided with four USEx containers, whereas in the second bioassay, the ten GFs were given the opportunity to oviposit in four water containers. At the end of the 7-day egg-laying period, all live females were checked for egg retention.

Data collection, processing, and statistical analysis

In all bioassays, oviposition responses were tracked according to previously published procedures (Satho et al. 2015) using a dissecting microscope (Meiji EMZ; Meiji Techno Co., Ltd., Tokyo, Japan). The total number of eggs deposited in each container replicate was determined by enumerating the eggs laid on the filter paper substrate and those deposited on areas not covered by the substrate. These data were used to compute mean values and percentages of eggs oviposited, the two parameters that were used to score oviposition responses. The numbers of eggs retained were counted for each live female by dissecting the ovaries under a microscope. As reported by Farjana and Tuno (2012), the total number of eggs produced by a female was defined as the sum of eggs laid and retained. Egg retention rate per female or during each no-choice bioassay was computed as the total number of eggs retained divided by the total of eggs produced × 100. The differentiations of oviposition and egg retention responses were detected by non-parametric test from Systat version 11 (2004), with $p < 0.05$ as score of statistical significance.

Results

Egg-laying responses to used sock medium in assorted competition with water

When provided with similar chances to lay eggs in two containers holding USEx and two others with water, *Ae. albopictus* females deposited eggs in all containers, but oviposition responses varied appreciably with container medium.

Of the 5306 eggs oviposited by the 120 females, 74.52% (3954/5306) and 24.80% (1352/5306) were laid in water and USEx containers, respectively. The mean number of eggs laid in containers filled with water (164.75 ± 16.54 eggs, range 64–364 eggs) was significantly greater than that deposited in USEx containers (56.33 ± 10.27 eggs, range 0–189 eggs) (Mann-Whitney test: $z = 56.00$, $p < 0.001$) (Fig. 2).

When egg deposition opportunities were biased toward containers with water, *Ae. albopictus* females exhibited skip oviposition, laying eggs in all four containers. Oviposition responses varied significantly with container medium (Mann-Whitney test: $z = 2.00$, $p = 0.008$). The total numbers of eggs deposited in water and USEx containers were 1190 and 80, corresponding to 93.70 and 6.3% of the total laid, respectively. The mean number of eggs deposited per water container (99.16 ± 14.48 eggs, range 35–194 eggs) was 4.95 times that in containers with USEx (20.00 ± 11.61 eggs, range 0–43 eggs) (Fig. 3).

When there were more choices to oviposit in USEx containers, *Ae. albopictus* females deposited eggs in all four containers, with greater preference for those holding water. Of the 1277 eggs, 114 (8.92%) were deposited in containers with USEx and 1163 (91.08%) in water containers. The mean number of eggs deposited in USEx containers (9.50 ± 4.56.54 eggs, range 0–57 eggs) was far lower than that laid in containers with water (290.75 ± 57.97 eggs, range 138–415 eggs) (Mann-Whitney test: $z = 0.00$, $p = 0.004$). There were 32.22 times more eggs oviposited in water containers than in the three USEx containers (Fig. 4).

Oviposition activity and egg holding in USEx and water environments

In the four water container no-choice oviposition experiments, a total of 2569 eggs were laid by the 40 females (water container 1, 164.75 ± 37.93; water container 2, 139.50 ± 41.17; water container 3, 192.50 ± 70.45; water container 4, 145.50 ± 36.68) at a mean of 64.22 (2569/40 females) per female. When four USEx containers were the unique oviposition sites, the 40 females laid a total of 259 eggs (USEx container 1, 7.50 ± 2.25; USEx container 2, 14.50 ± 9.21; USEx container 3, 14.00 ± 8.86; USEx container 4, 28.75 ± 16.38), corresponding to 6.47 eggs laid per female. Significantly more eggs were laid when four water containers were the only oviposition sites than in the four USEx container no-choice bioassay (Mann-Whitney test: $z = 1.00$, $p < 0.001$) (Fig. 5a; Table 1).

Ae. albopictus females retained eggs in both the four water container and four USEx container no-choice oviposition bioassays, but egg retention varied appreciably with the different egg deposition opportunities. When four containers with water were the unique oviposition sites, 26.31% (10/38) of the females retained eggs 7 days after blood meal uptake. A total of 405 eggs were found in the ovaries of 10 females at an average of 40.50 ± 8.51 eggs per female. In the four USEx container no-choice oviposition experiment, 97.36% (37/38) exhibited egg retention. A total of 2804 eggs were still kept in the 37 females 1 week postblood feeding at a mean of 75.78 ± 3.24 eggs per female. Egg retention by a female in the four USEx container bioassay was 1.89 times higher than that in the four water container bioassay. Gravid *Ae. albopictus* females presented with four USEx containers retained significantly more eggs than those that were given four water containers as egg deposition sites (Mann-Whitney test: $z = 16.00$, $p = 0.021$) (Fig. 5b).

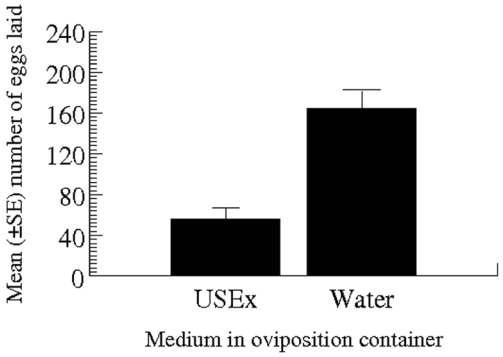

Fig. 2 Oviposition responses of females of *Ae. albopictus* when offered equal opportunities to lay eggs in two containers with used sock extract (USEx) and two others with water

Discussion

To our knowledge, this study represents the first trial to formally examine the effects of foot-derived materials—generally known to provide essential cues for blood-seeking females—against ovipositing female mosquitoes. Using a series of choice bioassays, we found that sites containing USEx were not attractive to ovipositing females of *Ae. albopictus*. We also observed that the rate of mature egg retention among females given opportunities to oviposit only in a USEx environment

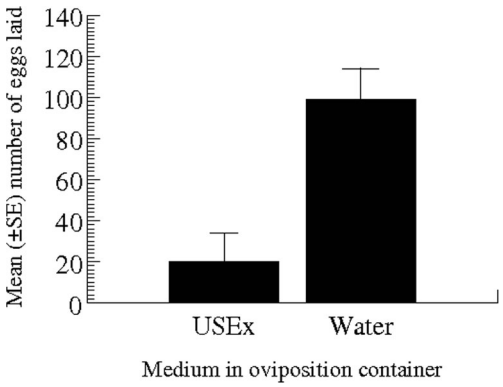

Fig. 3 Oviposition responses of females of *Ae. albopictus* when given less opportunities to lay eggs in containers with sock extracts (USEx) than in water

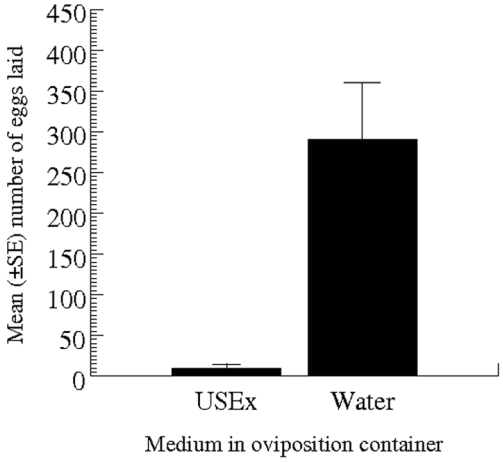

Fig. 4 Oviposition responses of females of *Ae. albopictus* when offered more opportunities to lay eggs in containers with sock extracts (USEx) than in water

was markedly higher than that of their counterparts presented with only water containers as egg deposition sites.

There was an obvious association between medium type and level of oviposition response. Gravid females exhibited decreased egg deposition in USEx oviposition sites when in competition with oviposition sites containing tap water. The appeal of potential breeding sites to ovipositing mosquito females is dependent upon many factors. In particular, olfactory cues (Navarro-Silva et al. 2009) are known to provide information about food resources (Ponnusamy et al. 2010; Obenauer et al. 2010) and suitability for completion of larval development (Reyes-Villanueva et al. 1990; Afify and Galizia 2014), which are major determinant factors in egg-laying site selection. Dengue mosquito females can differentiate between oviposition sites (Dieng et al. 2003; Zettel Nalen et al. 2013) and exhibit decreased egg laying in the presence of either oviposition deterrents (Xue et al. 2001; Satho et al. 2015), irritants, or repellents (Canyon 2001). This behavioral tactic could be a strategy to avoid unsuccessful embryo maturation and larval development; thus, any factor that causes such egg-laying avoidance may be a valuable candidate for control of dengue vectors.

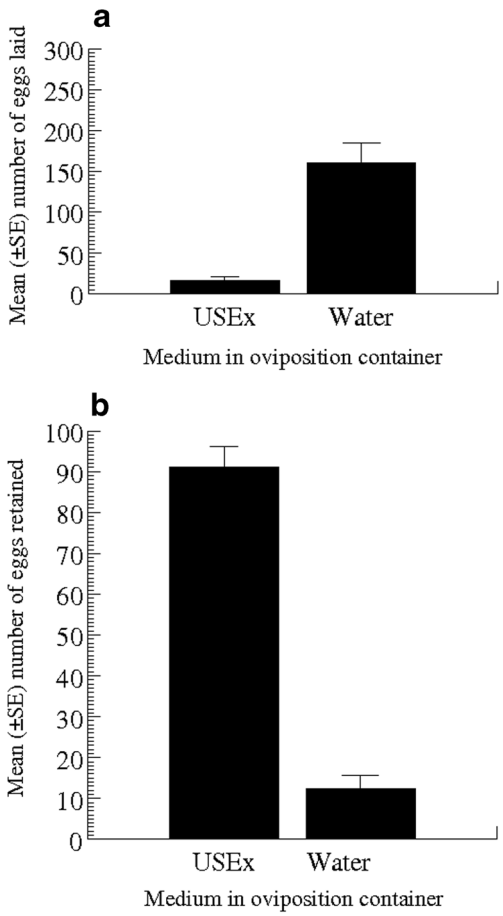

Fig. 5 Oviposition responses (**a**) and egg retention (**b**) by *Ae. albopictus* females in no-choice bioassays. Females were offered four containers with water or four containers with USEx (used sock extract)

The observed extremely weak oviposition responses of *Ae. albopictus* to USEx at all levels of competition between USEx and water containers corroborated earlier reports indicating that oviposition responses of dengue mosquito females showed negative correlations with some airborne substances from potential oviposition sites. For example, *p*-cresol, a volatile component of Bermuda grass (Allan and Kline 1995; Afify and Galizia 2014), and essential oil extracts from medicinal plants (Prajapati et al. 2005; Warikoo et al. 2011), notably monoterpenes and sesquiterpenes (Autran et al. 2009; Nerio et al. 2010), have been reported to reduce egg deposition activities of dengue vectors. Kramer and Mulla (1979) observed limited oviposition responses of *Culex* mosquitoes in habitats containing organic extracts, such as lab chow infusion. This reduction in egg deposition rate was credited to the presence of acetic, propionic, isobutyric, butyric, isovaleric, and caproic acids in the infusion that acted as repellents (Hwang et al. 1980). In fact, the decision to deposit eggs by gravid females is related to chemosensory cues that are detected via olfactory sensillae present in the antennae, mouthparts, wing margins, and legs (Bohbot and Vogt 2005; Santos et al. 2012). Seenivasagan et al. (2010) assessed the sensory aspects of ovipositional responses of dengue mosquitoes in relation to the chemical hexadecyl pentanoate and found increased rejection by ovipositing females. They suggested that the chemical acted as repellent by hampering the normal functioning of the antennal receptors that mediate olfaction.

Rejection of an oviposition site has also been related to the presence of predators (Wasserberg et al. 2013) and toxicants (Von Windeguth et al. 1971; Satho et al. 2015). Chemical (Verma 1986; Canyon 2001) and some microbial (Canyon 2001) insecticides have been reported to deter gravid dengue mosquito females from depositing eggs. In the present study, no predators were involved, and so differential egg-laying responses due to predation is unlikely. We used tap water

Table 1 Comparison of oviposition responses in relation to oviposition opportunities and egg retention

	Four water container bioassay	Four SE container bioassay
Total number of eggs laid	2569	259
Total number of eggs retained	405	2804
Total egg produced	2974	3063
Mean (±SE) egg retention rate (%)	12.278 ± 2.736	91.038 ± 4.350
Range	4.321–16.626	80.00–99.071

and an extract from used socks. Water has been shown to be not attractive to gravid *Aedes* females and is often used as a negative control in many oviposition behavior studies (Chadee et al. 1993; Satho et al. 2015). Although tap water only is unsuitable for offspring success, USEx containers showed lower attractiveness to ovipositing *Ae. albopictus* females than water containers even when there were more egg deposition opportunities in water. These differences in oviposition responses were likely related to features of USEx. Optically, the water was colorless, whereas USEx was light brown, a color known to be attractive to gravid females (Afify and Galizia 2014; Satho et al. 2015). One day after bioassays were set up, there was a strong smell when we approached the experimental cages, especially in the experiment involving three USEx containers per cage. For all bioassays, USEx was produced by soaking a pair of socks (that had been worn with shoes for 12 h) in 400 mL of tap water for 1 h, and the sieved solution was used immediately for bioassays. Socks are made from various materials including natural and synthetic materials (Abd El-Hady 2014; Tarbuk et al. 2011) and many chemicals (Tarbuk et al. 2015). They are designed to trap sweat, and for this purpose, many chemicals are used, some of which are highly toxic. These include zeolite and activated carbon (Tarbuk et al. 2015), the heavy metal copper (Abd El-Hady 2014), silver nanoparticles (Foltynowicz et al. 2013), and dyes (Opie et al. 2003).

Sweat contains several biochemical compounds and metabolites, i.e., sodium chloride, lactic acid, water, urea, uric acid, sebaceous gland secretions (Sato et al. 1989a, b), free amino acids (Kutyshenko et al. 2011), and nicotinic acid (Mickelsen and Keys 1943). Most of these products are nutrients for bacteria, and their actions produce a cocktail of different molecules, including butyric, caprylic, and caproic acids; ammonia; carbon dioxide (Huang et al. 2002); short-chain fatty acids (Kanda et al. 1990); methanethiol; propanoic acid; and isovaleric acid (Lukacs et al. 1991; Myriam 2009). These compounds are highly odorous. For example, ammonia has an irritating odor and is toxic for some organisms (Huang et al. 2002; Brinkman 2009). Propionic acid smells like the acetic acid in vinegar (Laing and Francis 1989) and isovaleric acid has a strong pungent odor (Ara et al. 2006). Methanethiol has a powerful garlic-like odor (Lin et al. 2005). When worn, socks come into direct contact with the feet. Wearing socks and shoes may produce more sweating and smell. In the present study, the nylon socks used to produce USEx were worn for 12 h. Although we did not assess the chemistry of the experimental socks, the fact that they were worn for a day and half means that they would have picked up many compounds. In support of this suggestion, it has been reported that socks trap many skin-derived chemicals for long periods (Sherwood 2011). In addition, the strong smell that emanated from USEx containers when sniffed or when standing near experimental cages indicated the presence of some of the odorous molecules mentioned above. In support of these suggestions, it has been demonstrated that nylon socks are effective for collecting, conserving, and dispensing foot odor (Njiru et al. 2006; Matowo et al. 2013).

There is evidence that deterrents or repellents present in oviposition sites cause forced egg retention in mosquitoes, including dengue vectors (Xue et al. 2005; Seenivasagan et al. 2010; Satho et al. 2015). Such egg retention is deleterious to fitness and reproductive output (Xue et al. 2001; Xue et al. 2005). Based on previous reports and our observations, it is clear that the presence of USEx affects the oviposition responses of *Ae. albopictus*, and it is likely that such effects occurred in a way that may be similar to that reported by Kramer and Mulla (1979) and Hwang et al. (1980). Furthermore, it is possible that the USEx medium contains substances from the sock material, shoe insole, skin bacteria, bacterial metabolites, or their combinations, which acted as repellents or deterrents against *Ae. albopictus*. Additional investigations are needed to identify such anti-egg-laying agents.

Xue et al. (2005) designated a competent oviposition repellent (piperidine or DEET: *N,N*-diethyl-3-methylbenzamide) as one that can cause >50% oviposition deterrence. In the present study, the four USEx container oviposition bioassay caused egg retention in over 97% of the females tested at an average of about 75 eggs per female, and a mean egg retention rate of 91%, and oviposition control outcome higher than that obtained by Xue et al. (2005). Tikar et al. (2014) examined the oviposition deterrent activities of diethyl phenyl acetamide and diethyl benzamide against vectors, including *Ae. albopictus*. Here, we extended this type of approach by evaluating USEx against gravid dengue mosquitoes to find repellent agents that are not only biorational but are also highly

available. The results of the present study indicated that the presence of USEx in container habitats causes a strong repellent effect against gravid *Ae. albopictus* females. In addition, this USEx repellence caused females to retain increased numbers of eggs, a phenomenon known to decrease reproductive outcomes in this species (Xue et al. 2005). Given that socks are footwear items and that foot areas and odorous socks attract mosquito bites due to sweat (DeJong and Knols 1995), an effect that has been explored to develop devices to lure host-seeking females (Matowo et al. 2013), the observed effects of USEx on gravid *Ae. albopictus* females were unexpected. USEx exhibited anti-egg deposition and egg retention inducer properties. Such attributes coupled with the documented egg retention effect on reproductive parameters (Xue et al. 2005) encourage the integration of used socks in dengue vector control programs.

Conclusions

Socks, which are commodity products worn on the feet, constitute an essential garment of daily life. About 70% of men wear socks daily (Transparency Market Research 2016). In general, socks can become odorous very rapidly, and rewearing has become an elective activity that is rarely adopted. Annually, huge amounts of socks are produced worldwide. Datang, the world's leading sock producer, makes nine billion pairs of socks each year (The Guardian 2012). Also, the demand for such commodity has been drastic in recent years (Wang 2009). In general, the useful life of socks is relatively brief and is even decreasing due to rapid changes in market and fashion trends (Staikos 2006) and our desire to wear clean socks. Used socks are usually discarded after a short period of time (Shortney 1976). Socks are made of various materials, some of which are toxic (Opie et al. 2003; Abd El-Hady 2014). Socks may contain spandex made of many chemicals, including toluene-2,4-diisocyanate (Groce 1999). To increase sweat absorption and antibacterial properties, many other chemicals, such as silver nanoparticles (Benn and Westerhoff 2008), organotin compounds (Greenpeace 2015), and coating materials (Horton 2001), are added to socks during the manufacturing process. When worn with shoes, socks may be contaminated with many toxicants present in the midsole (Dahlberg 2010). Silver nanoparticles are harmful to waste water treatment (Potera 2010). Socks can leach out up to 650 μg of silver (Benn and Westerhoff 2008). Nanoparticle silver is highly toxic to bacteria and aquatic life (Morones et al. 2005; Benn and Westerhoff 2008; McGeer et al. 2000). Organic tin compounds are lethal to mollusks (Kimbrough 1976). Toluene-2,4-diisocyanate is poisonous to humans and animals (US EPA 2016). Although many strategies have been developed to recycle used socks (Green Eco Services 2011; Jones 2015), the predicted increase in footwear consumption (Transparency Market Research 2016) and consequent incidence in sock waste and the potential adverse environmental impacts mean that new waste management strategies are needed. To anticipate these problems, we assessed the possibility of using soiled socks to control dengue mosquitoes. As used socks and foot odor have already been successfully explored as means of controlling host-seeking populations of malaria vectors (Njiru et al. 2006; Matowo et al. 2013; Mmbando et al. 2015), the finding that USEx repels gravid *Ae. albopictus* females and forces them to retain most of their eggs offers new avenues for the discovery of oviposition repellents or deterrents. In addition, this observation provides the impetus to encourage the incorporation of used socks as a new component in integrated approaches for dengue management. This study used extracts from used socks. However, we do not know if the obtained oviposition responses resulted from the sock-derived compounds or the sock bearer's foot-derived organic materials (sweat remnants and bacteria and/or their metabolites). Additional studies are needed to demonstrate whether or not *Aedes aegypti* gravid responded to compounds from the sock or human skin.

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