



Polarized light and oviposition site selection in the yellow fever mosquito: No evidence for positive polarotaxis in *Aedes aegypti*

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ABSTRACT

Aquatic insects and insects associated with water use horizontally polarized light (i.e., positive polarotaxis) to detect potential aquatic or moist oviposition sites. Mosquitoes lay their eggs onto wet substrata, in water, water-filled tree/rock holes, or man-made small containers/bottles/old tyres containing water. Until now it has remained unknown whether mosquitoes are polarotactic or not. The knowledge how mosquitoes locate water would be important to develop new control measures against them. Thus, we studied in dual-choice laboratory experiments the role of horizontally polarized light in the selection of oviposition sites in blood-fed, gravid females of the yellow fever mosquito, *Aedes aegypti*. On the basis of our results we propose that *Ae. aegypti* is not polarotactic. Thus the yellow fever mosquito is the first known water-associated insect species that does not detect water by means of the horizontally polarized water-reflected light. This can be explained by the reflection–polarization characteristics of small-volume water-filled cavities/containers preferred by *Ae. aegypti* as oviposition sites.

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1. Introduction

The yellow fever mosquito, *Aedes aegypti* is found throughout subtropical and tropical areas of the world and considered the major vector for the transmission of dengue and yellow fever. It is a largely diurnal-biting species (Chadee, 1988) that apparently uses chemical and visual cues to locate its host (Kawada, Takemura, Arikawa, & Takagi, 2005). Gravid mosquito females, generally, need to locate suitable bodies of water into which they can lay their eggs, so that their aquatic larvae can develop normally (Clements, 1963), and in this regard female *Ae. aegypti* are no exception. However, they are known to accept small and inconspicuous containers like tree holes and, in urban areas, flower vases, discarded tyres, cans, bottles, and paper cups as breeding sites (Seng & Jute, 1994). How they find water is still not fully understood.

Hygroreception is known to play some role in the oviposition of mosquitoes (Clements, 1999), and hygroreceptors have, indeed, been described from the mosquito antenna (Yokohari, 1999). However, these receptors can operate only over relatively short

distances. Another possibility therefore is that they use visual cues, since mosquitoes in flight are known to depend on optical inputs for orientation (Allan, Day, & Edman, 1987). Reflected light from water surfaces has been reported to influence oviposition site location by mosquitoes in the field (Belton, 1967). Moreover, Kennedy (1941) observed that gravid mosquitoes prepared for oviposition when flying over a mirror and some gravid mosquitoes were even seen to respond to the sight of water (Muirhead-Thompson, 1940) and the movement of mosquito larvae within it (McCrae, 1984).

In a series of observations Schwind (1985, 1991, 1995) discovered that several species of aquatic bugs and beetles are polarotactic, i.e. find water by means of the horizontal polarization of light reflected from the water surface. Later studies (Bernáth, Szedenics, Molnár, Kriska, & Horváth, 2001; Csabai, Boda, Bernáth, Kriska, & Horváth, 2006; Horváth, Bernáth, & Molnár, 1998; Horváth, Malik, Kriska, & Wildermuth, 2007; Horváth & Varjú, 2004; Kriska, Bernáth, & Horváth, 2007; Kriska, Csabai, Boda, Malik, & Horváth, 2006; Kriska, Horváth, & Andrikovics, 1998; Kriska, Malik, Szivák, & Horváth, 2008; Wildermuth, 1998; Wildermuth & Horváth, 2005) showed that beside numerous aquatic bugs and beetles also many other insect species associated with water (i.e. as larvae developing in water, but

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as adults being terrestrial), like dragonflies, mayflies and caddisflies, exhibit positive polarotaxis when searching for water. Until now no aquatic insect species has been found that would not select its aquatic habitat by positive polarotaxis.

According to the above, one could have expected mosquitoes to be also polarotactic, i.e., able to find appropriate aquatic or moist oviposition sites by means of the horizontal polarization of light reflected from the water surface or wet substrata (Horváth & Varjú, 2004). Although over the last decades the study of the biology of mosquitoes was intense (e.g. Clements, 1963, 1999) due to their offensive biting habits and role in spreading various dangerous diseases, it has remained unknown whether they are polarotactic or not. To know this could be of importance in developing new effective measures against them, since more and more mosquito populations become resistant to the pesticides used to control them (DARP, 2007; Kang et al., 1995).

Although some field and laboratory experiments had earlier been carried out to investigate colour preference and effect of substrate brightness on egg-laying in mosquitoes (e.g. Belton, 1967; Dhileepan, 1997; Jones & Schreiber, 1994; McCrae, 1984; Muir, Kay, & Thorne, 1992a; Muir, Thorne, & Kay, 1992b; Wen, Muir, & Kay, 1997; Williams, 1962), mosquito polarization sensitivity was only sporadically studied (Kalmus, 1958; Kovrov & Monchadskiy, 1963; Wellington, 1974). Thus, we investigated in double-choice laboratory experiments the role of horizontally polarized light in the selection of the oviposition site in blood-fed, gravid females of the yellow fever mosquito, *Aedes aegypti*, one of the most dangerous and wide-spread mosquito species in the world. Earlier studies on the eyes of mosquitoes have not given any indication of the existence of polarization sensitivity in the ventral eye region (e.g., Brammer, 1970; Brammer, Stein, & Anderson, 1978; Clements, 1963, 1999; Land, Gibson, Horwood, & Zeil, 1999; Muir et al., 1992b; Sato, 1959).

2. Materials and methods

Ae. aegypti imagoes were obtained from a laboratory colony kept in the Plant Protection Institute of the Hungarian Academy of Sciences, Budapest. Larvae in rearing dishes were fed with powdered cat food. Emerging adults copulated in a separated cage, in which they were maintained at $28 \pm 5^\circ\text{C}$ and 30–40% relative humidity under a day:night regimen of 16:8 h light:dark. Females were blood-fed on caged mice twice a week.

One double-choice and two pilot experiments were carried out in the laboratory to reveal the possible role of linearly polarized light in the egg laying of *Ae. Aegypti*. Groups of adult gravid female mosquitoes were placed into a dark test cage immediately after blood feeding. They were kept there for 72 h before being returned to the breeding cage. Resting, blood-fed, female mosquitoes needed about 48–60 h to mature their eggs (Clements, 1999). Although some eggs were deposited during the first 48 h, most were laid during the third 24-h period.

All experiments were carried out in the same test cage (length = 50 cm, width = 40 cm, height = 40 cm) placed in a windowless darkened room. A small access window (10 cm \times 10 cm) on one of the sidewalls was used for introducing gravid, blood-fed female mosquitoes. The cage was equipped with two square illuminating windows (10 cm \times 10 cm, 8 cm apart) in the immediate vicinity of the back wall of the test cage (Fig. 1A). Both windows were transilluminated through a combination of sheet polarizers and depolarizers (Fig. 1C). The test cage was arranged in such a way that the illuminating windows were vertical (Fig. 1A). During the experiments the windows provided a moderate, 40 lux illumination of the chamber (measured by a Gossen Starlite multifunctional light detecting instrument) that allowed mosquitoes to fly and oviposit actively. To ensure a sufficiently high ambient light intensity was important, because *Ae. aegypti* is diurnal and thus needs some light to be active during daytime. To avoid unwanted polarization of light reflected from the inner surfaces of the test cage, all these surfaces were wrapped by white, matt dry filter paper, which was always replaced before every choice experiment with a new mosquito group.

In all experiments two Petri dishes filled with dechlorinated clear tap water were offered for egg laying. An open-surface dish supplied with distilled water from a small tank (both covered outside by matt white dry filter paper) was used to replenish the evaporated water through communicating vessels, which also maintained constant water level in the Petri dishes during the tests. The replenishing open-surface dish was placed near the access window on the opposite side of the

test cage (Fig. 1A) to keep relative air humidity homogeneous throughout the cage. The homogeneous distribution of air humidity eliminated the possibility that positive polarotaxis could be overridden by positive hygrotaxis in the test chamber.

Since *Aedes* species are known to lay eggs individually only on moist substrata (Clements, 1999), the Petri dishes were supplied with 18 cm long and 2 cm high vertical annular strips of white filter paper on their perimeters (Fig. 1B). These paper strips were continuously wet during the experiments. In the first pilot experiment we confirmed that a water surface screened by dry matt/shiny, black/white reflecting surfaces, acting as an invisible source of high air humidity and dry test surfaces with different reflection–polarization characteristics, were insufficient to elicit egg laying, because *Ae. aegypti* females need direct contact with a wet surface for oviposition under any illumination condition, including total darkness. As a control, in our second pilot experiment we presented a water-filled Petri dish (with a wet paper strip) and an empty Petri dish (with a dry paper strip) transilluminated from below by unpolarized visible and ultraviolet light, and counted the eggs laid onto the paper strips. We found that gravid, blood-fed yellow fever mosquitoes oviposited exclusively onto the wet paper strip of the water-filled Petri dish, telling us that the mosquitoes could discriminate. This showed that our experimental conditions were appropriate.

The Petri dishes were put next to the side-windows (Fig. 1A). Since the photoreceptors of *Ae. aegypti* are either green-, or ultraviolet-sensitive (Snow, 1980), the test cage was equipped to operate with separate visible (400 nm $< \lambda$) and UV ($\lambda < 400$ nm) transilluminations of the windows. During the choice experiment and the videopolarimetric measurement of the polarization patterns of the stimuli (Fig. 2) the test cage was in darkness and light stimulus entered only through the two bottom-windows. The polarization patterns in Fig. 4 were also measured by videopolarimetry, the method of which has been described in detail elsewhere (Horváth & Varjú, 1997).

In the dual-choice experiment polystyrene Petri dishes with a diameter of 8 cm were placed next to the side-windows separated by a vertical wall under another horizontal sheltering wall, both wrapped by matt white dry filter paper (Fig. 1A). This arrangement ensured that the water surface in the Petri dishes did not reflect vertically polarized light (being possibly neutral or repellent for female mosquitoes); it reflected only unpolarized or weakly horizontally polarized light according to the characteristics of the side illumination. All mosquitoes flying below the horizontal sheltering wall had to choose between the two separated, exactly horizontally polarized and unpolarized light sources. Although the illuminating light came from the side rather than from the water surface, this circumstance did not prevent the mosquitoes from oviposition. Polarized and unpolarized combined vis + UV transilluminations of the side-windows were produced by means of the combination of UV-transmitting polarizers and depolarizers (Fig. 1C).

In the dual-choice experiment test groups of 5–30 blood-fed female mosquitoes were placed into the test cage for 3 days. The number of eggs laid on the outer (convex) and inner (concave) sides of the wet paper strips in the Petri dishes (Fig. 1B) were counted under a microscope and divided by the number of females to reduce variance. Since *Ae. aegypti* females usually lay eggs on wet surfaces (Clements, 1999), eggs found in the water were considered to be washed off from the inner surface of the wet paper strips. The average number of eggs laid onto the wet paper strips by mosquitoes of any given group was analysed by two-way ANOVA (Sokal & Rohlf, 1981) to examine the possible preference of Petri dishes illuminated from the side by totally horizontally polarized light or unpolarized light, and the possible preference of left or right Petri dishes. Normality of the data was checked by Kolmogorov–Smirnov test (Sokal & Rohlf, 1981).

3. Results

In our dual-choice experiments with gravid females of *Ae. aegypti* egg-laying occurred 48–72 h after blood-feeding. Since the average number of eggs laid by females was highly variable (mean = 26.5, standard deviation = 16.3), we were forced to use relatively large groups of mosquitoes in the tests. Table 1 provides information on the number of females in the experiments, the number of mosquito groups, the total number of eggs laid, and the average number of eggs per female laid onto the wet paper strips in the Petri dishes illuminated from the side by totally horizontally polarized and unpolarized visible and ultraviolet light.

In the experiments blood-fed, gravid female mosquitoes preferred the concave inner surface of the wet paper strips. The spatial distribution of the eggs laid was always homogeneous and random on the wet paper strips. The degree of linear polarization d ($\approx 0\%$ or 100%) of light illuminating the two Petri dishes from the side had no influence on the number of eggs laid per female (Fig. 3A, Table 1). Neither the left, nor the right position of the Petri dish proved to be significantly more attractive to the mosquitoes in our experiments (Fig. 3B, Tables 1 and 2).

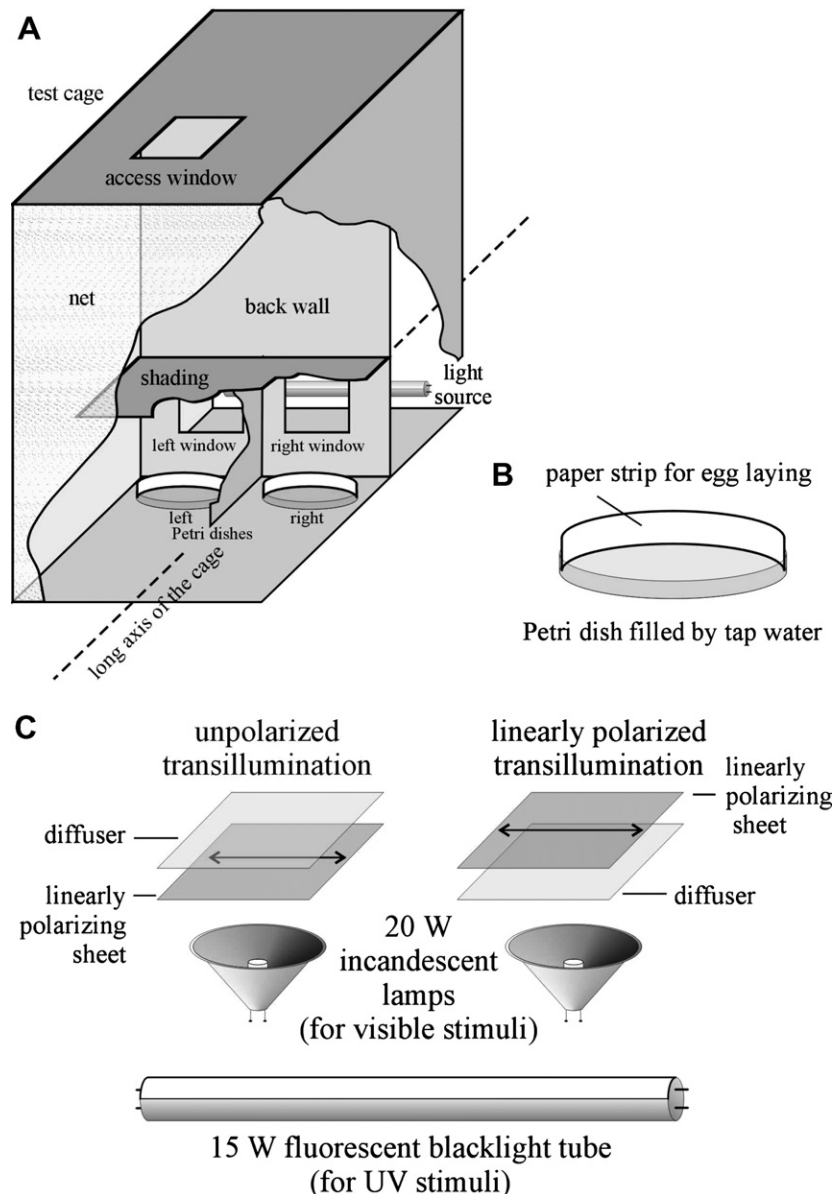


Fig. 1. Arrangement of the dual-choice experiment performed with female *Ae. aegypti*. (A) Geometry of the test cage with side-windows. (B) A Petri dish with a wet paper strip for egg laying. (C) Method of the production of unpolarized and linearly polarized transilluminations.

4. Discussion

Based on the above results, we conclude that linearly polarized light with horizontal or oblique directions of oscillation does not influence the choice of the oviposition site in blood-fed, gravid *Ae. aegypti* females. This negative behavioural result suggests that *Ae. aegypti* may be the first example of an insect species associated with water, which does not use polarotaxis to detect water.

Our mosquito-study was the first in which the polarization characteristics of the stimuli were properly controlled and the polarization cue available to the mosquitoes tested was separated from radiance and colour. We admit, however, that there was one major difference between our experimental setup and the natural habitats and oviposition sites of *Ae. aegypti*: The degree of linear polarization d of the stimuli was very high ($\approx 100\%$) and independent of the viewing angle, whereas for water surfaces seen from above and from low elevations d approaches zero. Thus, under diffuse illumination, for an insect flying over a small body of water,

the water surface will first appear unpolarized, at the Brewster angle maximally polarized, when directly above the water unpolarized, later strongly polarized again, and finally, on leaving, unpolarized. This gradient of d was missing in our artificial polarized light stimuli.

However, until now no aquatic insect species has been found that would use the d -gradient of water-reflected polarized light for water detection. Even the contrary has been shown for the backswimmer, *Notonecta glauca*: Schwind (1985) demonstrated that the polarotactic *Notonecta* detects water on the basis of the strong and horizontal polarization of light reflected from water approximately at the Brewster angle, rather than by means of the d -gradient of the reflection-polarization pattern of the water surface. A similar alignment (Brewster angle) of the field of view of the ventral polarization-sensitive eye region is not excluded in other aquatic insect species. Hence, there is no evidence that would support the hypothesis that the d -gradient of the water surface could play a role in the water detection by aquatic insects, including mosquitoes. Note, however, that the uprising of *Notonecta* as it

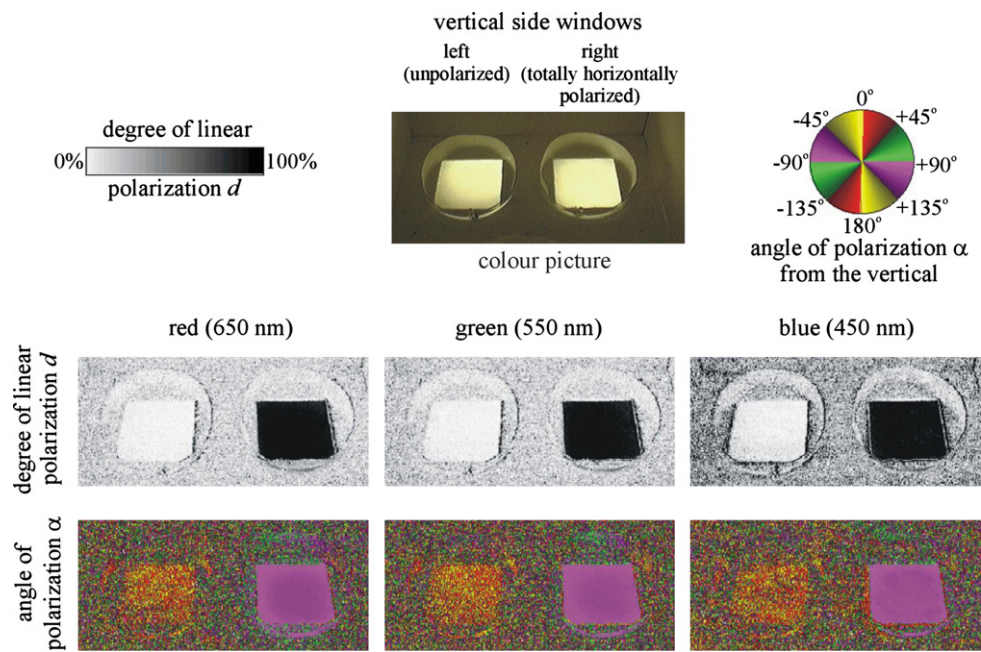


Fig. 2. Colour picture and patterns of the degree of linear polarization d and angle of polarization α of the side windows of the test cage measured by videopolarimetry in the red (650 nm), green (550 nm) and blue (450 nm) parts of the spectrum. The left/right window was transilluminated by unpolarized/totally and horizontally polarized light. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

Table 1

Number A of *Ae. aegypti* females in the dual-choice experiment, number G of mosquito groups, total number E of eggs, and average number N of eggs per female laid onto the wet paper strips in the two Petri dishes illuminated from the side by totally horizontally polarized, and unpolarized vis + UV light

Illumination number	Linearly polarized				Unpolarized	
	A	G	E	N	E	N
	181	10	1462	8.1	1519	8.4

approaches a water body is just one (and the only) example where a gradient analysis seems improbable. The high degree of linear polarization d should not be a problem either, because most often super-natural (or supernormal) stimuli with horizontal direction of polarization are preferred by polarotactic aquatic insects to the natural situations (Bernáth et al., 2001; Csabai et al., 2006; Horváth & Varjú, 2004; Horváth et al., 1998, 2007; Kriska et al., 1998, 2006, 2007, 2008; Schwind, 1985, 1991, 1995; Wildermuth, 1998). Thus, our experiments, which used artificial polarized stimuli, were suitable for ruling out an attractive effect of reflection polarization on water-seeking *Ae. aegypti* females.

Table 2

Statistical results of the two-way ANOVA (Sokal & Rohlf, 1981) of the average number N of eggs per female laid by *Ae. aegypti* onto the wet paper strips in the two Petri dishes illuminated from the side by totally horizontally polarized, and unpolarized visible + ultraviolet light

	SS	DF	MS	F	p
Intercept	1318.319	1	1318.32	48.036	<0.001
Position	6.566	1	6.566	0.239	0.631
Polarization	0.016	1	0.016	0.001	0.981
Error	466.552	17	27.444	—	—

SS, sums of squares; DF, degree of freedom; MS, mean squares; F , calculated F -values; p , significance levels of F -probes; intercept, interactions between the main effects; position, effect of the position (left or right) of the Petri dish in the test cage; polarization, effect of the polarization characteristics of the transillumination; error, variation unexplained by the main effects.

Fig. 4 shows the reflection–polarization patterns of three suitable egg-laying sites of mosquitoes. Depending on the direction of reflection with respect to the open water surface, d of light reflected from lakes and ponds is high, relative to that of light reflected from water plants (Fig. 4A and B). On the other hand, the direction of polarization of light reflected from both the water sur-

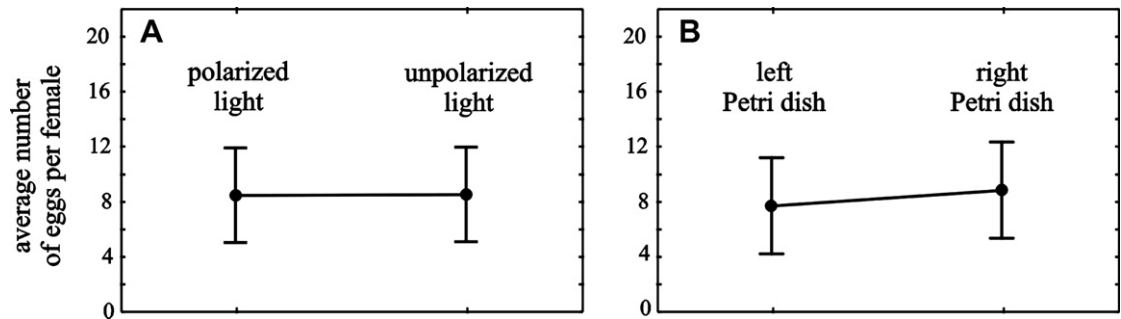


Fig. 3. (A) Average numbers of eggs per female laid by groups of *Ae. aegypti* onto the wet paper strips in the two Petri dishes illuminated from the side by totally horizontally polarized, and unpolarized vis + UV light. (B) Average numbers of eggs per female in the left and right Petri dishes. Dots show the average number of eggs per female, and the vertical bars indicate the 95% confidence intervals.

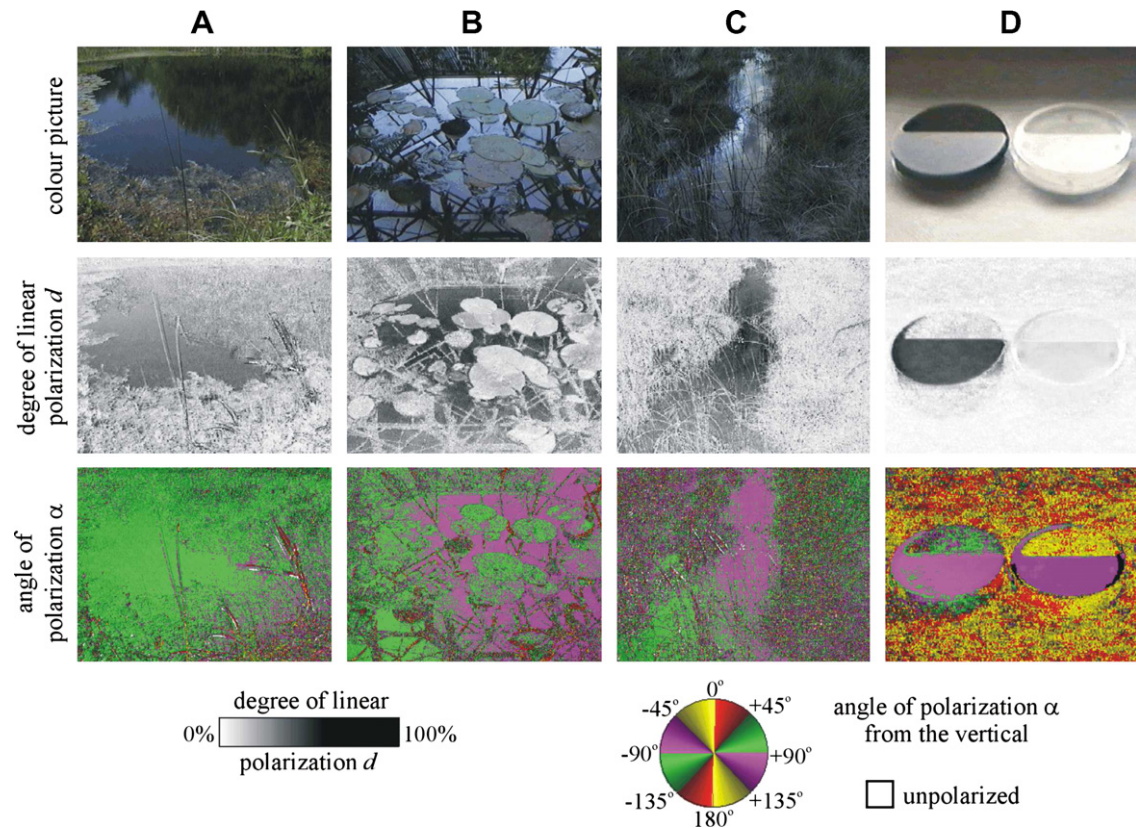


Fig. 4. Colour pictures and patterns of the degree of linear polarization d and angle of polarization α of three typical oviposition sites of *Ae. aegypti* measured by videopolarimetry in the green (550 nm) part of the spectrum. (A) A lake with water plants close to the shore. (B) A small lake with dense growth of water lilies on the water surface. (C) A rapidly drying, shiny wet mud surface of a grassy field in a marshy area. (D) Glass Petri dishes filled with black oil (left) and clear water (right) on a white substratum, demonstrating the reflection–polarization characteristics of dark and bright water in small containers. The upper halves of the dishes are shaded, the lower halves lit by unpolarized white light from an overcast sky. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

face and the horizontal leaf blade of a water plant is horizontal. Hence, there exists a relatively high difference in d between the water surface and the water plants. The same holds true for wet mud (Fig. 4C). The d of light reflected from the surrounding vegetation and soil is low and its direction of polarization is not always horizontal due to the random orientation of the elementary reflectors associated with vegetation and soil. Hence, there are considerable differences in both degree and direction of polarization of reflected light between open water or wet mud and the surroundings.

From afar, water bodies and wet substrata with open surfaces can be detected most effectively by means of the horizontal polarization of reflected light (Figs. 4A–C). The d of light reflected from vegetation, ground and soil is generally low, and the direction of polarization is not always horizontal. On the other hand, d of light reflected from water surfaces and wet substrata at the Brewster angle (about 37° from the horizontal for water) is high and the direction of polarization is always horizontal. This is the reason why aquatic insects can use positive polarotaxis when searching for open water (Horváth & Varjú, 2004; Schwind, 1985, 1991, 1995).

Until now no fly (Diptera) species has been shown to possess a ventral polarization-sensitive eye region. Blood-fed, gravid mosquito females need to find water, because their eggs have to be laid in water or on wet soil. In search of hosts or water *Ae. aegypti* can fly even 17 km per night for example (Briegel, 2003). Hygroreceptors are known to play a role in the oviposition of mosquitoes (Clements, 1963, 1999), and if *Ae. aegypti* searches areas of generally high humidity, it may easily find water surfaces. On the other hand, one could also assume that yellow fever mosquito females, like other aquatic insects and insects associated with water, could detect water

by means of positive polarotaxis. However, according to our experiments, horizontally or obliquely polarized light do not play a role in the oviposition site selection by blood-fed, gravid *Ae. aegypti* females. Although polarotactic water detection is widespread among mayflies, dragonflies, caddisflies, aquatic beetles and bugs (Horváth & Varjú, 2004), it is less useful for *Ae. aegypti* for at least two reasons:

- Under natural conditions *Ae. aegypti* prefer water-filled cavities and shallow bodies of waters with a dense growth of aquatic plants. Such water bodies usually reflect light with low d and sometimes with vertical direction of polarization (Fig. 4D, right water-filled Petri dish) (Bernáth, Szedenics, Wildermuth, & Horváth, 2002). Muddy or marshy soils, also acceptable to *Ae. aegypti* as egg-laying sites, are strong polarizers only if they are sufficiently wet, but their polarizing characteristics rapidly diminish when they dry out (Horváth & Varjú, 2004).
- In nature, *Ae. aegypti* oviposit also in rain water accumulations of tree and rock holes. These tiny water bodies reflect light with low d , because their surfaces are generally in the shade (see the shaded regions of both Petri dishes in Fig. 4D). Under unnatural (urban/peridomestic) conditions *Ae. aegypti* preferentially breed in container habitats, like opaque bottles, discarded containers, old tyres and other small-volume cavities (Diarrassoula & Dossou-Yovo, 1997). In these artificial containers too, the water surfaces are generally shaded, consequently reflecting only weakly (and not always horizontally) polarized light (Fig. 4D).

From the above we can conclude that the water in the mentioned natural or man-made small holes, preferred by *Ae. aegypti* as oviposition sites, cannot be found on the basis of the polarization of

water-reflected light. This could be one of the reasons why the oviposition site selection of this mosquito species was not influenced by horizontally or obliquely polarized light in our choice experiments. The absence of polarized light orientation might be expected for an insect that oviposits in small ponds with lots of vegetation.

On the other hand, there is some evidence that the olfactory detection of semiochemicals may indicate an oviposition site to *Ae. aegypti* (e.g., Bentley & Day, 1989; Ganesan, Mendki, Suryanarayana, Prakash, & Malhotra, 2006). Moreover, hygrosensors in the antennae of mosquitoes have been reported (e.g., Yokohari, 1999). The detection of semiochemicals and hygroreception in *Ae. aegypti*, in combination with the documented preferences for dark places (Muir et al., 1992a, for example, reported that *Ae. aegypti* prefer red and black targets, while blue, yellow and white ones are unattractive), may play a significant role in the recognition of small, hidden water bodies as oviposition sites.

We would like to emphasize that our finding that *Ae. aegypti* is not polarotactic, does not disprove the possibility that other mosquito species detect their aquatic or moist habitats and egg-laying sites by the horizontal polarization of water-reflected light. Dhileepan (1997) surveyed the physical and chemical cues influencing egg-laying behaviour of *Culex annulirostris* and *C. molestus*. He found that these mosquitoes preferred water-filled containers with black bottoms. Wen et al. (1997) found similar colour preferences in *C. quinquefasciatus*: black and brown targets were most attractive in both visible and UV spectral ranges. Several other field and laboratory experiments were carried out to test the effect of brightness on oviposition behaviour in different mosquito species (*Culex*: Belton, 1967; *Aedes*: Williams, 1962; *Toxorhynchites*: Jones & Schreiber, 1994). Consistently the darker (water or artificial) surfaces were preferred. Note that in these experiments the most attractive, i.e., darker surfaces also had the highest polarizing characteristics. Thus, the possible role of positive polarotaxis in these experiments cannot be excluded. Unfortunately, the reflection–polarization characteristics of the mentioned test surfaces were never measured. Therefore it would be worth studying whether other mosquito species, especially those that develop in open waters (e.g., *Anophelini*), or deep in the water (e.g., *Mansoniini*) use polarization of reflected light to identify those habitats most suitable for their larvae. It would also be interesting to investigate, whether mosquito species closely related to *Aedes* (e.g., *Aedini*) are or are not polarotactic.

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