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Polarotaxis in non-biting midges: Female chironomids are attracted to horizontally polarized light

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ABSTRACT

Non-biting midges (Chironomidae, Diptera) are widely distributed aquatic insects. The short-living chironomid adults swarm in large numbers above water surfaces, and are sometimes considered a nuisance. They are vectors of certain bacteria, and have a key-role in benthic ecosystems. Optical cues, involving reflection-polarization from water, were found to be important in the habitat selection by three Mediterranean freshwater chironomid species. In this work we report on our multiple-choice experiments performed in the field with several other European freshwater chironomid species. We show that the investigated non-biting midges are positively polarotactic and like many other aquatic insects their females are attracted to horizontally polarized light. Our finding is important in the visual ecology of chironomids and useful in the design of traps for these insects.

1. Introduction

The family Chironomidae (Diptera) is the most widely distributed, most diverse, and often the most abundant of all aquatic insect families [1]. Short-living adults of chironomid species (non-biting midges) can be observed mainly on the days when great numbers of these unnervingly mosquito-like insects swarm all over the waterfronts. Periodic mass swarming can even harm the reputation of given beaches affecting negatively the local tourism, thus chironomids are sometimes considered as nuisance pests. Swarming non-biting midges may also play a role as vector species transferring bacteria from infected water bodies to clear ones. Egg-batches were found to host *Vibrio cholerae* bacteria in great numbers [2].

On the other hand, non-biting midges have a key-role in freshwater benthic ecosystems [1]. Huge masses of their aquatic larvae dwell on the bottom of water bodies feeding on organic debris and bacteria, and serving as a basis of benthic food webs. Emerging adults remove significant amounts of biomass from natural water bodies, which facilitates the natural cleaning of waters by reducing their total carbon amount and phosphorus content. Moreover, their carcasses transfer surplus organics present in water to nearby areas, increasing also the fertility of arable land. These ecological and economical roles render highly important any factor governing the abundance and distribution of non-biting midges, especially egg-laying females. Optical cues, including reflection-polarization were found to be important in three Mediterranean freshwater chironomid species [3–5], and polarized light was regarded as one of the possible factors in breeding habitat selection by the females of these chironomids. Although it has been described yet that certain chironomid species are attracted to horizontally polarized light, it actually has been documented in only one serial of studies [3–5]. At the same time the role of positive polarotaxis in finding places for oviposition by chironomids is not clear in all aspects, since Lerner et al. [4] found that it could be modified by other factors such as habitat availability and density of specimens.

Many aquatic insects (the adults and larvae of which live in water) and several insects associated with water (whose larvae develop in water, but the adults are terrestrial) [3,6–12] detect their habitat by means of the horizontal polarization of light reflected from the water surface [13–17]. Thus, they are usually attracted to various natural [6,7,9] or artificial [18–26] sources of horizontally polarized light. This behaviour is called positive polarotaxis. Information on the generality of polarotaxis in chironomids is highly needed to assess the applicability of polarized-light-traps or the measures affecting the reflection-polarization characteristics of water surfaces. In this work we report on our multiple-choice experiments performed in the field with non-biting midges. We show here that the females of several

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further chironomid species of the temperate zone, beyond the three Mediterranean freshwater species studied earlier [3–5], are also attracted to horizontally polarized light. This finding is important with regard to the visual ecology of non-biting midges and useful in the design of traps catching these insects.

2. Materials and methods

Experiment 1 was performed at Dömörkapu (47° 40′ N, 19° 03′ E) in the Danube-Ipoly National Park. It was done between 5 and 8 June 2010, every day from 18 to 21 h in the immediate vicinity of a mountain creek running parallel to an asphalt road. During the 4-day experiment the site (being in the shadow of trees and a mountain near sunset) was illuminated by light from the clear sky. The investigated adult chironomids emerged from the creek. Four test surfaces were put on the roof (150 cm from the ground level) of a red car (Daewoo Matiz, Fig. 1). One of the test surfaces was a matte black cloth and the other a matte white cloth. The material of both cloths (50 cm × 70 cm) was of common linen (bed-sheet). The other two test surfaces were a black and a white plastic tray (50 cm × 50 cm) filled with clear, transparent common sunflower-seed oil available in every food shop. The surface area of the cloths was slightly larger than that of the oil trays in order to overrepresent unpolarizing or weakly polarizing matte test surfaces being unattractive to all known polarotactic insects. In spite of their larger surface, both cloths were totally unattractive to chironomids. The positions of the four test surfaces on the car roof were randomized during replications. We used sunflower-seed oil, because in our earlier field experiments [27–30] we experienced that this liquid can trap effectively insects touching its surface. The oil surfaces used had two functions: (i) to capture the landing chironomids (in the case of the white and black oil-filled trays), and (ii) to act as reflectors providing highly and horizontally polarized light at the Brewster angle in the case of the black oil-filled tray. We used only black and white test surfaces (trays and cloths), because they were colourless, thus eliminated the possible interference between colour and polarization vision in chironomids. The four test surfaces were put on the car roof, because in a pilot experiment we observed that numerous chironomid species were attracted to the roof, where they performed sexual behaviour (nuptial dance, water touching and copulation) being typical in chironomids only above water surfaces. The rationale of this experiment was to study whether (i) horizontally polarized light is the relevant optical cue for chironomids lured to a car, and (ii) the more or less polarizing test surfaces with different brightnesses can elicit positive polarotaxis in chironomids if the sources of polarized light are at a height above the ground level. The oil-filled trays captured every chironomids touching its surface, and at the end of every experiment we counted the trapped chironomids (Tables 1 and 2). One of the authors (A. Móra) determined taxonomically the captured chironomids (Table 1). On the other hand, the matte cloths could not trap them. Thus, during every experiment we observed visually the behaviour of chironomids above the matte test surfaces and counted their touch-downs. Chironomids' landings counts on the cloth surfaces were made by eye. We could not use any adhesive (e.g., "Tanglefoot") to trap landing chironomids, because such adhesives or glues would make the originally matte test surfaces shiny, inevitably resulting in reflection-polarization. However, the function of the matte black and

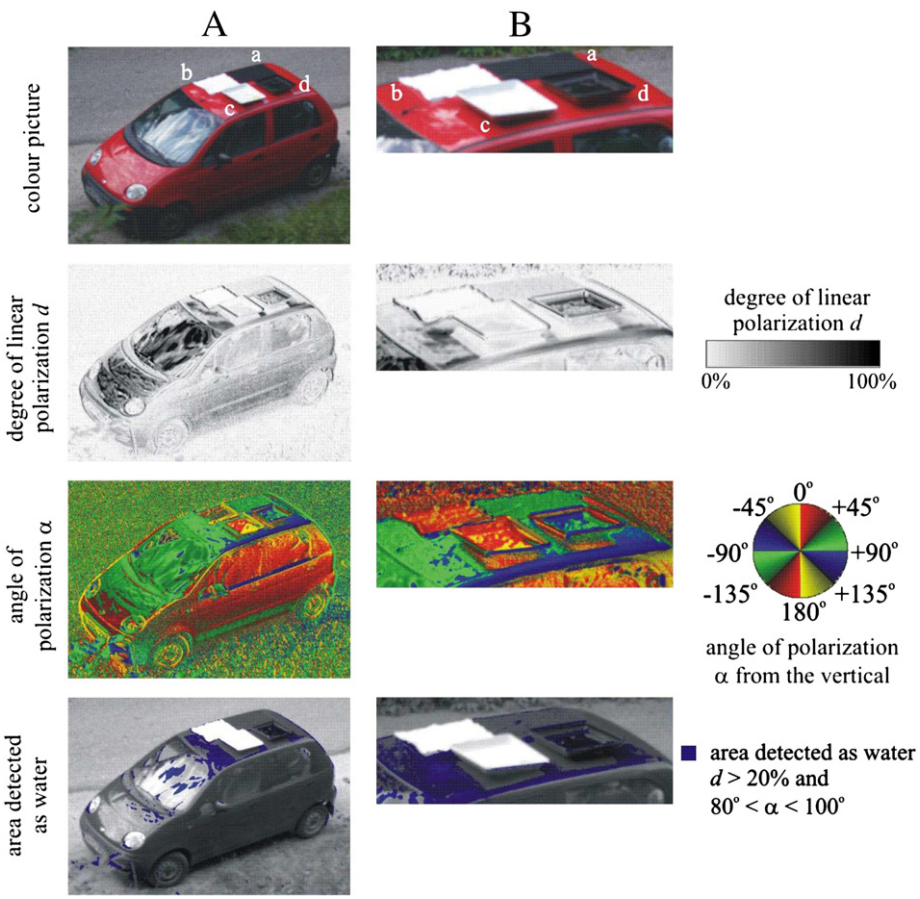

Fig. 1. Colour picture, patterns of the degree of linear polarization d and angle of polarization α (clockwise from the vertical), and areas detected as water (d>20%, 80°<α<100°) measured in the green (550 nm) part of the spectrum for the test surfaces (a: matte white cloth, b: matte black cloth, c: salad-oil-filled white tray, d: salad-oil-filled black tray) used in experiment 1 with chironomid flies. During the experiment the test surfaces were put onto the roof of a red car, the scene was illuminated by skylight from the clear sky. The angle of elevation of the optical axis of the polarimeter was −25° (A), and −15°(B) from the horizontal.

Table 1
Species, number and sex (f: female, m: male) of chironomids trapped by the black and white trays filled with salad-oil and laying on a car roof in our experiment 1, and p-values for two different χ^2 statistical tests. Tests were performed to separately compare numbers of males and females of all species collected by black or white oil trays. As a second test the summed numbers of individuals belonging to all species were compared.

Chironomid taxa	Oil-filled tray		χ^2 test p, df = 1 black–white pairs separated for sexes	χ^2 test p, df = 1 black–white pairs summed for sexes
	Black	White		
Chironomidae spp. (8 species)	f = 20 m = 0	f = 0 m = 0	<0.001 –	<0.001
Chironominae sp. (1 species)	f = 45 m = 0	f = 1 m = 0	<0.001 –	<0.001
Chironomus riparius	f = 545 m = 21	f = 6 m = 1	<0.001 <0.001	<0.001
Micropsectra atrofasciata	f = 75 m = 5	f = 0 m = 0	<0.001 0.025	<0.001
Micropsectra notescens	f = 80 m = 5	f = 0 m = 0	<0.001 0.025	<0.001
Rheocricotopus atripes	f = 0 m = 4	f = 0 m = 0	– 0.046	0.046
Sum	f = 765 m = 36	f = 7 m = 1	<0.001 <0.001	<0.001

white cloths was just to provide test surfaces with no or very weak reflection-polarization (that is to reduce drastically the degree of linear polarization of reflected light). The temperature of the test surfaces was measured with a digital contact thermometer with an accuracy of ±0.25 °C.

Experiment 2 was conducted between 9 and 12 June 2010. It was the repetition of experiment 1 in such a way that the test surfaces were on a dry asphalt road (Fig. 2, Table 2), instead of a car roof, and there was no car in the vicinity. In experiment 2 the positions of the four test surfaces on the asphalt road were again randomized during replications. In this experiment we tested whether polarotaxis is also present in the absence of the complex optical cues of a car body, but in the presence of a homogeneous weakly and horizontally polarizing asphalt surface (running through the biotope of the investigated chironomids). During this 4-day experiment the site (being the same as that of experiment 1) was again illuminated by skylight. We collected the trapped chironomids after every experiment, by which we performed 4 replications (Table 2). Since the differences between the captures were statistically highly significant (Table 2), further replications were unnecessary. In this experiment the chironomids trapped by the black and white oil-filled trays were counted without a later taxonomical determination. In experiment 2 the trapped specimens have not been identified at species level nor sexed (which is a difficult task), because this experiment was performed immediately after experiment 1 at the same site, thus the same species with similar sex ratios can be assumed.

Table 2
Number of chironomids trapped by the black and white trays filled with salad-oil and laying on the ground in our experiment 2, and p-values for χ^2 statistical test. Tests were performed to separately compare numbers of males and females of all species collected by black or white oil trays. As a second test the summed numbers of individuals belonging to all species were compared.

Date (2010)	Oil-filled tray		χ^2 test p, df = 1 black–white pairs summed for sexes
	Black	White	
9 June	253	2	<0.001
10 June	189	1	<0.001
11 June	169	4	<0.001
12 June	188	2	<0.001
Sum	799	9	<0.001

2.1. Imaging polarimetry

The reflection-polarization characteristics of the test surfaces were measured in the red (650 nm), green (550 nm) and blue (450 nm) parts of the spectrum by imaging polarimetry when they were illuminated by light from the clear sky. The method of imaging polarimetry and its calibration have been described in detail elsewhere [9,31]. The reflection-polarization patterns (Figs. 1 and 2) were measured for three different angles of elevation θ of the polarimeter: (i) When the test surfaces were on the car roof (experiment 1), θ was −25° (Fig. 1A) and −15° (Fig. 1B). In these cases the polarimeter was set up on a hill slope near the car. (ii) When the test surfaces were put on an asphalt road in experiment 2 (to ensure a greater absolute value of θ) near the car (Fig. 2), θ was −34°, coinciding practically with the Brewster angle (at which the degree of linear polarization d of reflected light is maximal, $\theta_{Brewster} = \text{arccotan}\, n = 33.7°$ for salad-oil with an index of refraction of $n = 1.50$). An area of a polarizing reflector is sensed as water by polarotactic chironomids (as by aquatic insects in general), if (i) the degree of linear polarization d of reflected light is higher than a threshold d^*, and (ii) the deviation $\Delta\alpha = |90° - \alpha|$ of the angle of polarization α from the horizontal ($\alpha = 90°$) is smaller than a threshold $\Delta\alpha^*$ [9,28]. Both thresholds d^* and $\Delta\alpha^*$ depend on species [12]. Based on our earlier experiences, in Figs. 1 and 2 we used the values of $d^* = 20\%$ and $\Delta\alpha^* = 10°$. Although these threshold values are rather arbitrary, the use of other values did not influence qualitatively our results and conclusions.

2.2. Statistics

To examine the divergence of numbers of chironomid taxa trapped by the black and white oil-filled trays representing a hypothesized uniform distribution, χ^2 tests were performed [32]. Statistical tests were performed using the STATISTICA 6.0 software.

3. Results

In both experiments the chironomids neither touched nor landed on the matte white and black test surfaces. Although chironomids swarmed with a quick flight above the matte cloths, we could observe with the naked eye that they obviously did not touch these matte surfaces. A very few (8 and 9) chironomids were trapped by the white oil-filled tray, while the black oil-filled tray captured numerous (801 and 799) individuals (Tables 1 and 2, Fig. 3). In experiment 1 the black and the white oil trays captured 765/36 = 21.3 and 7 times more females than males, respectively. We identified the following four species in the trays: *Chironomus riparius*, *Micropsectra atrofasciata*, *M. notescens*, *Rheocricotopus atripes*; 8 additional chironomids and one chironomine could not be identified (Table 1). All species were statistically highly significantly more attracted to the black tray ($N = 801$) than the white ($N = 8$). Similar results were obtained in experiment 2 when the test surfaces were on an asphalt road at ground level (Table 2): the black tray was 1600/17 ≈ 94 times more attractive to chironomids than the white one, and the asphalt surface was not touched by chironomids. In experiment 2 the captured chironomids were neither identified, nor sexed. Since this experiment was performed at the same site and immediately after experiment 1, it is logical to assume that the same chironomid species with a similar sex ratio occurred in both experiments. Hence, the investigated chironomids were attracted practically only to the black oil-filled tray, independently of the height of the test surfaces.

According to our polarimetric measurements (Figs. 1 and 2, Tables 3 and 4), the car roof, the black oil-filled tray, the horizontal matte black cloth and the horizontal dry asphalt surface reflected horizontally polarized light in the red, green and blue parts of the spectrum. On the other hand, the direction of polarization of light reflected from the white oil-filled tray and the matte white cloth was vertical in the red

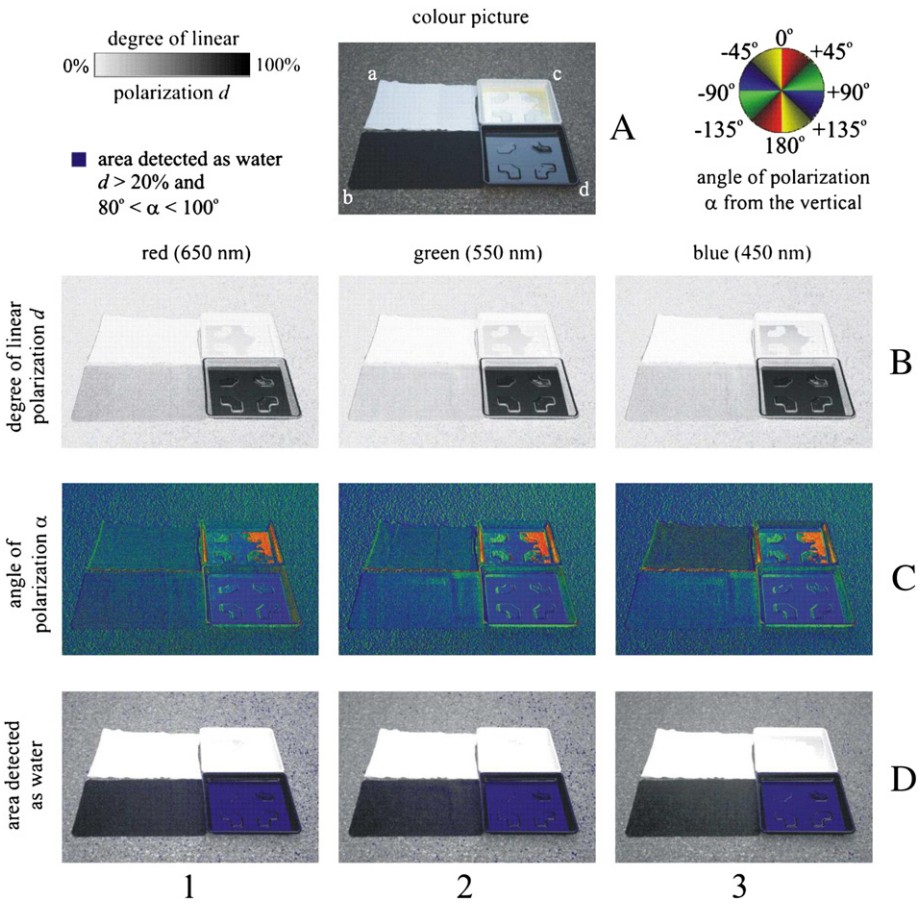

Fig. 2. Colour picture (A), patterns of the degree of linear polarization d (B) and angle of polarization α (clockwise from the vertical) (C), and areas detected as water (d>20%, 80°<α<100°) (D) measured in the red (1), green (2) and blue (3) parts of the spectrum for the test surfaces (a: matte white cloth, b: matte black cloth, c: salad-oil-filled white tray, d: salad-oil-filled black tray) used in experiment 2 with chironomids. The test surfaces were put onto a dry asphalt road, the scene was illuminated by skylight from the clear sky, and the angle of elevation of the optical axis of the polarimeter was −34° from the horizontal.

and green spectral ranges, and it was horizontal only in the blue part of the spectrum (Table 3). Certain parts of the car body (including the roof) reflected highly polarized light (with degrees of polarization d>50%, Table 4) in the green and blue spectral ranges, depending on the local tilt (curvature) of the car surface. The matte white cloth and the white oil-filled tray reflected very weakly polarized light (d<10%, Table 3), the matte black cloth and the grey asphalt surface reflected weakly polarized light (d<18%, Tables 3 and 4), while the black oil-filled tray reflected highly polarized light (d>60%, Table 3), depending on the angle of elevation from the horizontal. The consequence of these reflection-polarization characteristics was that only the black oil-filled tray and certain regions of the car roof were mistaken for water by these polarotactic aquatic insects (coloured by blue in the last row of Figs. 1 and 2). This shows that the studied chironomids, attracted only to the black tray, are positively polarotactic insects, being attracted to horizontally polarized light.

In both experiments the temperature of the four test surfaces was always the same and coincided with the air temperature.

Fig. 3. Photograph of chironomid specimens (Table 1) trapped by the black salad-oil-filled tray used in our choice experiments.

4. Discussion

One of the novelties of our work is that our results presented here strongly support the generality of polarotaxis in chironomids: we

Table 3
Degree of linear polarization d (%) and angle α (°) of polarization (clockwise from the vertical) of light reflected from the black and white test surfaces (oil-filled trays and matte cloths) used in experiments 1 and 2 and measured by imaging polarimetry in the red (650 nm), green (550 nm) and blue (450 nm) parts of the spectrum.

Spectral range	Optical variable	Test surface			
		Black oil tray	White oil tray	Matte black cloth	Matte white cloth
Red (650 nm)	d (%)	65.9 ± 10.6	4.1 ± 1.0	15.0 ± 3.5	1.7 ± 1.0
	α (°)	89.8 ± 5.0	0.1 ± 5.6	90.0 ± 15.1	0.2 ± 16.2
Green (550 nm)	d (%)	69.1 ± 12.4	4.8 ± 1.3	15.3 ± 3.8	1.9 ± 1.0
	α (°)	90.0 ± 5.3	0.2 ± 5.9	90.2 ± 13.5	0.0 ± 15.4
Blue (450 nm)	d (%)	75.4 ± 13.2	5.2 ± 1.5	17.5 ± 4.6	2.1 ± 1.1
	α (°)	90.1 ± 5.2	90.2 ± 7.1	90.1 ± 14.2	90.3 ± 7.4

Table 4
Degree of linear polarization d (%) and angle α (°) of polarization (clockwise from the vertical) of light reflected from the red car roof and the dry asphalt surface used as substrates in experiments 1 and 2, respectively, and measured by imaging polarimetry in the red (650 nm), green (550 nm) and blue (450 nm) parts of the spectrum.

Spectral range	Optical variable	Substrate	
		Red car roof	Asphalt
Red (650 nm)	d (%)	10.5 ± 4.8	12.1 ± 6.3
	α (°)	90.8 ± 5.2	90.3 ± 16.2
Green (550 nm)	d (%)	53.3 ± 16.7	13.4 ± 6.7
	α (°)	90.2 ± 5.8	90.0 ± 15.1
Blue (450 nm)	d (%)	65.1 ± 17.4	15.2 ± 7.1
	α (°)	90.5 ± 6.4	89.5 ± 17.3

extended the number of known polarotactic chironomid species from three [3–5] to more than its double (Table 1). If in our experiments the choice of the investigated chironomids had been governed by positive phototaxis, they should have been attracted to both white (matte and shiny) test surfaces (white cloth and white oil-filled tray). But neither white test surfaces were attractive. If the choice of chironomids had been governed by negative phototaxis, they should have been attracted to both black (matte and shiny) test surfaces (black cloth and black oil-filled tray). But this was not the case. We found that female chironomids were attracted practically exclusively to the black oil-filled tray reflecting always highly and horizontally polarized light at the Brewster angle. Thus, we conclude that the females of the studied chironomids (Table 1) possess positive polarotaxis, as many other aquatic insect species [9].

Our test surfaces were always of the same temperatures, so that potential temperature effects in the choice by chironomids could be excluded. Since the test surfaces were shaded and not lit by direct sunlight, the black oil tray and black cloth were not warmer than the white oil tray and white cloth, as it would be the case in a sunlit situation.

In our experiments the sticky oil captured all chironomids in the trays, whereas the cloth surface allowed them to survive and be recounted elsewhere. However, this could not bias our results, because we counted only the touch-downs of chironomids. Chironomids did not land on the matte white and black cloth surfaces, and the white and black oil surface captured at once all chironomids touching the oil surface.

The roles of the odour and colour of the oil in the choice of chironomids studied in our field experiments can be excluded, because the same type of sunflower-seed oil was used in both black and white trays. Similarly, the odour of the used cloths was also irrelevant in the choice of chironomids, because the same kind of matte linen cloth (bed-sheet) was used. Only the brightnesses (black, white) of the colourless oil trays and matte cloths had been different in order to exclude the role of positive or negative phototaxis.

The 7 and 21 times larger numbers of female versus male chironomids captured by the oil trays could be explained by the fact that after copulation females look for oviposition sites by polarotaxis and during egg-laying they touch the water surface. However, touching the surface of the sticky oil in our experiments, they became inevitably captured. Male chironomids may also be positively polarotactic, but they do not lay eggs and thus do not touch the water surface (or the oil surface in our experiments). Other phenomena could also contribute to the dominance of females captured in our experiments: Protandry is well documented but not universal in chironomids. It was not found in some Orthocladiinae, for example [33]. On the other hand, unbalanced sex ratios (65–70% females) were observed in some *Tanytarsus*[34], but in other congeneric species sex ratios did not differ significantly from 1:1 [35]. Moreover, chironomids often copulate in aerial swarms, and after copulation males sometimes return to the swarm, while females fly away from the swarming site to deposit their eggs [36]. The species collected by us belong to different taxonomic groups which can vary in these characteristics. This fact linked with the unusual high female dominance (93–100%) captured by our oil trays suggests that positive polarotaxis plays a significant role in the behaviour of female chironomids. Another possibility for the biased sex ratio observed in our choice experiments could be the male/female differences in eye structure and function. Like many other insects, chironomids also may exhibit eye sexual dimorphism. In the chironomid *Belgica antarctica*, for example, males have a 25% greater photoreceptive area than females [37].

The investigated chironomids (Table 1) were attracted to the horizontally polarizing test surfaces (black oil-filled trays) placed on the ground or above the ground (car roof at a height of 150 cm). Jäch [38], Nilsson [19], Kriska et al. [39], van Vondel [20], Bernáth et al. [40] and Kriska et al. [41] have observed a similar attraction of aquatic insects to car roofs. In our experiment 1 we also observed a few individuals of some aquatic insects (mayflies and diving beetles). Aquatic insects (e.g. Coleoptera and Heteroptera) often swarm in large numbers, mate in air and land on the roofs, bonnets and boots of black or red cars; Ephemeroptera and Odonata females, moreover, often lay their eggs *en masse* on these car surfaces [41]. Dragonflies have also been observed to swarm above cars [18,21–24,40,42–45]. All these observations demonstrate that horizontally polarizing surfaces attract numerous aquatic insect species.

Our finding that the females of the investigated chironomid species (Table 1) are positively polarotactic can be useful for field entomologists studying the biology and ecology of these insects, because these investigators can design new chironomid traps reflecting highly and horizontally polarizing light, and thus attracting these insects. A prerequisite for the design and use of such polarization traps is the knowledge of polarotaxis in the target species. Here we showed for several chironomid species (Table 1) that their females are positively polarotactic, and thus can be lured to traps emitting/reflecting horizontally polarized light.

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