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SHORT COMMUNICATION

Ventral polarization vision in tabanids: horseflies and deerflies (Diptera: Tabanidae) are attracted to horizontally polarized light

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Abstract Adult tabanid flies (horseflies and deerflies) are terrestrial and lay their eggs onto marsh plants near bodies of fresh water because the larvae develop in water or mud. To know how tabanids locate their host animals, terrestrial rendezvous sites and egg-laying places would be very useful for control measures against them, because the hematophagous females are primary/secondary vectors of some severe animal/human diseases/parasites. Thus, in choice experiments performed in the field we studied the behavior of tabanids governed by linearly polarized light. We present here evidence for positive polarotaxis, i.e., attraction to horizontally polarized light stimulating the ventral eye region, in both males and females of 27 tabanid species. The novelty of our findings is that positive polarotaxis has been described earlier only in connection with the water detection of some aquatic insects ovipositing directly into water. A further particularity of our discovery is that in the order Diptera and among blood-sucking insects the studied tabanids are the first known species possessing ventral polarization vision and definite polarization-sensitive behavior with known functions. The polarotaxis in tabanid flies makes it possible to develop new optically luring traps being more efficient than the existing ones based on the attraction of tabanids by the intensity and/or color of reflected light.

Keywords Diptera · Tabanidae · Horsefly · Deerfly · Polarization vision · Positive polarotaxis · Water detection · Tabanid traps

Introduction

The tabanid flies (Diptera: Tabanidae, including horseflies of the genus *Tabanus* and deerflies of the genus *Chrysops*, as the economically two most important tabanid genus) have a world-wide distribution. Adult tabanids feed on nectar and pollen, and the females usually feed also on blood which aids the development of their eggs. Since the females suck also the blood of domestic animals and humans, the biology and behavior of tabanids have been intensely studied (e.g., Tashiro and Schwardt 1953; Hayakawa 1980; Hall et al. 1998; Lehane 2005). Tabanids are of particular importance also for the veterinary science and human health, because their hematophagous females are also primary or secondary vectors of some animal and human diseases and/or parasites, including tularemia, anaplasmosis, hog cholera, equine infectious anemia, filariasis, anthrax, and Lyme disease (Foil 1989; Luger 1990).

Tabanid females usually lay their eggs on marsh plants next to freshwater bodies, because after egg hatching the larvae must drop down into water or onto mud, where they develop (Tashiro and Schwardt 1953). To know how

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tabanids locate their host animals, terrestrial rendezvous sites and egg-laying places would be very useful for control measures against them. Several different traps have been designed to catch tabanids (e.g., Malaise 1937; Gressitt and Gressitt 1962; Catts 1970; von Kniepert 1979; Hribar et al. 1992; Moore et al. 1996; Mihok 2002). According to Allan et al. (1987), the hematophagous female tabanids can find their host animals by odors, heat, and visual cues. In spite of these studies, the optical cues relevant in the search for hosts, rendezvous, and oviposition sites of tabanids are only poorly understood (Thorsteinson et al. 1965; Lehane 2005).

Although polarization sensitivity is a fundamental sensory ability in numerous insects (Homberg 2004; Horváth and Varjú 2004; Wehner and Labhart 2006), until now no attention has been paid to the possible role of polarization vision in tabanids. With choice experiments performed in the field we investigated the polarotaxis in both males and females of 27 tabanid fly species, that is, whether, they are attracted to horizontal surfaces reflecting horizontally polarized light.

Materials and methods

The locality of our choice experiments 1–4 was a cemetery in the Hungarian town Kiskunhalas (46° 43′ N, 19° 5′ E). Our studies were carried out in this cemetery, because it was a convenient area where tabanids were abundant. Although there were a few garden taps in the cemetery, water surfaces did not exist. The cemetery is surrounded by family houses, where domestic animals are kept in large numbers. Ten meters from the cemetery, horses are kept in a horse school. The next natural water bodies are small alkaline lakes (with an area of ca. 20×30 m) at a distance of about 2 km from the cemetery on the periphery of the town. In the surroundings of Kiskunhalas there are numerous farms with sheeps, goats, cows, and horses. The tabanids observed and studied in the cemetery might have emerged from the mentioned water bodies, and might have lived either in the neighboring horse school, or in the vicinity of domestic animals. During the experiments the weather was calm, warm (the maximum/minimum daily temperature was 35–38°C/25–26°C) and sunny with clear or partly cloudy sky.

The first choice experiment was performed on 11 July (from 13:45 to 17:15 h = UTC + 2, where UTC is Universal Time Code) and 12 July (from 9:15 to 16:30 h) 2006 to study the polarotaxis in tabanids. Five dry test surfaces (1× 1 m) were laid horizontally onto the grassy ground 1 m apart (Fig. 1a). They were composed of a wooden board covered by a (1) shiny black plastic sheet, (2) shiny white plastic sheet, (3) aluminum foil, (4) matt black cloth, and (5) matt white cloth. Their orders were randomly changed hourly. Since in direct sunshine the black test surfaces would have become too warm, a constantly shaded place was selected in the cemetery as the site of the experiment. The sky was open above the test surfaces, the temperature T of which was measured with a digital contact thermometer: T of all test surfaces was always the same and coincided with the air temperature (within an accuracy of ±0.25°C). The behavior of tabanids at the test surfaces was continuously observed from a chair at a distance of 3 m. The tabanids attracted to the test surfaces were counted as a function of time. If a tabanid landed on a test surface, the time spent on it was measured by a digital stop watch. Sometimes the tabanids touched several times some of the test surfaces prior to landing. These touch-downs were also counted. Sometimes the tabanids flew up then landed several times on the same test surface within 1 s. These ‘flying-up’ events were also counted.

The second choice experiment was performed to demonstrate that tabanids are not attracted to vertical surfaces reflecting non-horizontally (vertically or obliquely) polarized light. In this experiment, done on 14 July 2006 between 9 and 14 h (UTC+2) at the same shady place as the first experiment, we used only the shiny black and white plastic sheets as test surfaces, because in the first experiment they turned out to be the first and second most attractive materials to tabanids; the other three test surfaces were practically unattractive (Table 1). Both test surfaces were either horizontal or vertical, 1 m apart and their order was switched every 30 min, while their horizontal or vertical direction was changed hourly. The vertical test surfaces faced always toward the antisolar meridian. The reactions of tabanids to both test surfaces were continuously observed and documented from a distance of 3 m.

After the first and second experiment (Tables 1 and 2), on 14 July 2006 between 14:00 and 18:00 (UTC+2) 43 tabanid flies were captured from the black plastic sheet with a common fly-net and conserved in alcohol for later identification. To examine the divergence of data in Tables 1, 2 and 3 from a hypothetized uniform distribution, χ^2-tests were performed (Sokal and Rohfl 1995).

In the third choice experiment we asked which eye region in tabanids is responsible for the positive polarotaxis discovered in the first and second experiments. Six different sticky traps were left in shady places in the cemetery between 08:00 h (UTC+2) on 4 July 2007 and 19:00 h on 6 July 2007. Each trap was composed of a white polystyrol board (50×50×5 cm) covered entirely either with a shiny black or a shiny white plastic sheet. The first trap pair (one black and one white) was placed horizontally onto the grassy ground, and their upward-facing surfaces (50× 50 cm) were covered with a color- and odorless transparent glue (BabolnaBio® mouse trap). The second trap pair was hung up horizontally onto tree branches at a height of

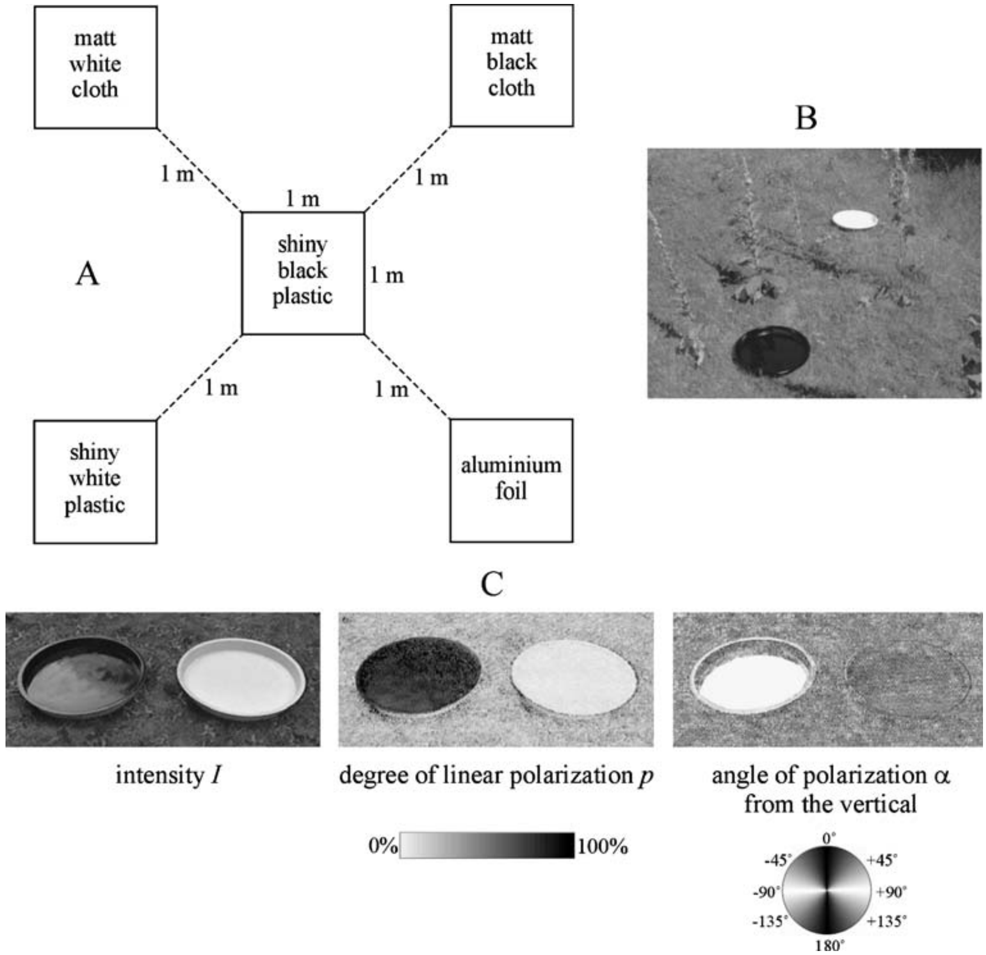

Fig. 1 **a** Arrangement of the five horizontal dry test surfaces used in the first choice experiment, during which the order of the test surfaces was randomized hourly. **b** Photograph of the black and white trays filled with salad oil in the fifth choice experiment at Erdőkertes. **c** Intensity I and patterns of the degree p and angle α of linear polarization of light reflected from the white and black plastic trays used in the fifth experiment and measured by video-polarimetry in the *blue* (450 nm) part of the spectrum. Quite similar patterns were obtained in the *red* (650 nm) and *green* (550 nm) spectral ranges. The trays were shady and illuminated by skylight. The optical axis of the polarimeter was −35° from the horizontal and viewed perpendicularly to the solar meridian

190 cm, and their downward-facing surfaces were covered with glue. The third trap pair was hung up vertically onto tree branches at a height of 190 cm, and both of their vertical surfaces were covered with glue. The horizontal distance between both members of a given sticky trap pair was 2 m, and the trap pairs were about 20 m apart horizontally well visible from a distance and from many different directions of view in the cemetery. The positions of the two members of each trap pair were switched every 2 h during the day. Between sunset and sunrise the positions of the traps were constant, since then tabanids do not fly. After this experiment the insects trapped by the

Table 1 Results of the first experiment with tabanid flies using five 1×1 m horizontal test surfaces

Test surface	Duration (s)		Number		
	$\sum t$	τ_{min}, τ, τ_{max}	$\sum N_T$ Touching	$\sum N_F$ Flying-up	$\sum N_I$ Individuals
Aluminum foil	170 (3.6%)	5, 12.1, 45	3 (0.2%)	20 (5.8%)	14 (6.9%)
Matt white cloth	45 (0.9%)	4, 9.0, 27	0 (0%)	5 (1.5%)	5 (2.5%)
Matt black cloth	23 (0.5%)	3, 2.9, 5	10 (0.6%)	6 (1.7%)	8 (3.9%)
Shiny white plastic	331 (6.9%)	7, 18.4, 75	30 (1.8%)	80 (23.3%)	18 (8.9%)
Shiny black plastic	4,203** (88.1%)	7, 26.6*, 189*	1,611** (97.4%)	233** (67.7%)	158** (77.8%)

Time $\sum t$ is the sum of the periods spent by all individuals between landing on and leaving the test surface. τ_{min}, τ and τ_{max} are the minimum, average and maximum of the period spent by an individual on the test surface. The numbers $\sum N_T$ and $\sum N_F$ of touching and flying-up, as well as the numbers $\sum N_I$ of individuals landing on the test surfaces are also given. Statistically significant differences between the corresponding data belonging to the shiny black plastic and other materials were marked (χ^2-test, df=4). The percentages relative to the total times/numbers are given in parentheses

*$p<0.05$

**$p<0.001$

Table 2 As Table 1 for the second experiment using only two test surfaces

Test surface	Duration (s)		Number		
	$\sum t$	$\tau_{\min}$, τ, $\tau_{\max}$	$\sum N_T$ Touching	$\sum N_F$ Flying-up	$\sum N_I$ Individuals
Shiny white plastic	91 (6.0%)	4, 13.0, 33	5 (0.6%)	39 (37.1%)	7 (8.7%)
Shiny black plastic	1426** (94.0%)	5, 19.5*, 215*	834** (99.4%)	66* (62.9%)	73** (91.3%)

These data were gathered when both surfaces were horizontal. Statistically significant differences between the corresponding data belonging to the shiny white and black plastic were marked (χ^2-test, df=1)
*$p<0.05$
**$p<0.001$

six sticky traps were conserved in alcohol for later identification. Although during the experiment the weather was calm, due to some slight air convections the hanging vertical/horizontal traps sometimes slightly rotated to and fro around their vertical symmetry axis, during which, however, their surfaces remained nearly vertical/horizontal.

In the fourth choice experiment we studied the water touching behavior of tabanids. One black and one white plastic tray with a diameter of 70 cm were laid horizontally onto the grassy ground of the cemetery. The trays were filled by clear tap water with a height of 4 cm. Both trays were always in shadow and 1 m apart. Their positions were switched every 2 h. The reactions of tabanids to both artificial water surfaces were observed from a distance of 3 m between 11:30 and 17:40 h (UTC+2) on 3 July 2007, and between 13:40 and 18:10 h on 7 July 2007.

In the fifth choice experiment we tested the capturing efficiency of a prototype of a new tabanid trap based on the positive polarotaxis in tabanids. This experiment was conducted at five different Hungarian places (Erdőkertes, Pécsely, Kiskunhalas 1 and 2, and Balatonszemes) being typical biotopes of tabanids. At every site one black and one white plastic tray with a diameter of 70 cm was laid horizontally 2 m apart onto the grassy ground which was either shady or sunny during the day (Fig. 1b, c). Both trays were filled by a light yellow salad oil to a height of 4 cm. According to our earlier experiences (Horváth et al. 1998; Horváth and Varjú 2004), salad oil can trap all insects that touch its surface. Between sunset and sunrise both trays were covered with a wooden board to avoid the trapping of night-active insects. Apart from the second place in Kiskunhalas, the positions of both trays were changed every 2 h from sunrise to sunset. At the second place in Kiskunhalas the trays were left from 26 June to 19 August 2007 in a garden of a family house, 2 km away from the cemetery. In the garden the positions of the trays were

Table 3 Number and sex (F, female; M, male) of the tabanids trapped by the black and white trays filled with salad oil in the 5th experiment performed at five different Hungarian sites, the geographic coordinates (latitude, longitude) of which are given together with the dates of the experiments, and the number *s* of species captured from the following 24 ones: *Atylotus fulvus*, *A. loewianus*, *Chrysops caecutiens*, *C. divaricatius*, *C. viduatus*, *Hybomitra acuminata*, *H. lundbecki*, *H. nitidifrons confusa*, *H. tropica*, *Heptatoma pellucens*, *Haematopota pluvialis*, *Tabanus bifarius*, *T. bovinus*, *T. bromius*, *T. cordiger*, *T. exclusus*, *T. glaucopis*, *T. maculicornis*, *T. miki*, *T. spectabilis*, *T. spodopternus*, *T. sudeticus*, *T. tergestinus*, *T. unifastiatus*

Site (latitude, longitude), date (2007)	Tray filled with salad oil					
	Black			White		
	F	M	F+M	F	M	F+M
Erdőkertes (47° 40′ N, 19° 19′ E), 8–9 July, *s*=20 (1 *Atylotus*, 3 *Chrysops*, 1 *Heptatoma*, 1 *Haematopota*, 4 *Hybomitra*, 10 *Tabanus*)	392	241	633**	10	6	16
Pécsely (46° 57′ N, 17° 47′ E), 20–21 July, *s*=8 (2 *Atylotus*, 6 *Tabanus*)	47	20	67**	4	2	6
Kiskunhalas 1 (46° 43′ N, 19° 5′ E), 28–29 June, *s*=7 (1 *Chrysops*, 6 *Tabanus*)	45	15	60**	1	2	3
Kiskunhalas 2 (46° 43′ N, 19° 5′ E), from 26 June to 19 August, *s*=7 (1 *Heptatoma*, 6 *Tabanus*)	8	18	26**	0	0	0
Balatonszemes (46° 49′ N, 17° 47′ E), 16–17 July, *s*=7 (1 *Chrysops*, 6 *Tabanus*)	12	4	16**	0	0	0
Total	504**	298**	802** (97.0%)	15	10	25 (3.0%)

Statistically significant differences between the corresponding data belonging to the black and white tray were marked (χ^2-test, df=1). In the last row the percentages relative to the total numbers of trapped tabanids are given in parentheses
**$p<0.001$

switched every day, and the trays were covered by a wooden board from sunset to sunrise, or when it was raining. The oil-trapped insects were conserved in alcohol. The captured tabanid species were identified by one of the authors (J. M.) on the basis of Majer (1987). The geographical coordinates (latitude, longitude) and dates of these experiments are given in Table 3.

The reflection-polarization characteristics of the dry and sticky test surfaces and the water- or salad-oil-filled trays (Fig. 1c) were measured by videopolarimetry in the red (650±40 nm=wavelength of maximal sensitivity±half bandwidth of the CCD detectors of the polarimeter), green (550±40 nm) and blue (450±40 nm) parts of the spectrum at the place of the choice experiments. The method of videopolarimetry has been described in detail elsewhere (Horváth and Varjú 1997). The elevation angle of the optical axis of the polarimeter was -35° from the horizontal, and the polarimeter looked perpendicularly to the solar meridian.

Results

The reflection-polarization characteristics of our test surfaces were independent of the wavelength of light, because they were colorless. The horizontal dry shiny black plastic sheet, the horizontal sticky black plastic sheet, the water- and salad-oil-filled black trays (Fig. 1c) reflected horizontally polarized light with very high degrees p of linear polarization (p=70%±20%=average±standard deviation). The horizontal shiny white plastic sheet, the horizontal sticky white plastic sheet, the water- and salad-oil-filled white trays reflected vertically or obliquely polarized light with very low degrees of polarization (p=10%±10%) or unpolarized light (p=0%). Both the vertical sticky black and white plastic sheets reflected non-horizontally (vertically or obliquely) polarized light with p_{black}=70%±20% and p_{white}=10%±10%. The horizontal aluminum foil reflected light with medium degrees of polarization (p=30%±15%) and diverse but usually non-horizontal directions of polarization. The horizontal matt white cloth, matt black cloth, and matt light brown wooden board reflected unpolarized light (p=0%).

In the first and second choice experiments we captured the following nine tabanid species (both females and males) on the horizontal black plastic sheet: *Haematopota pluvialis*, *Heptatoma pellucens*, *Hybomitra ciureai*, *H. solstitialis*, *H. ucrainica*, *Tabanus bovinus*, *T. bromius*, *T. sudeticus*, and *T. tergestinus*. The total number of caught males (26) was about 150% of that of females (17).

All tabanids behaved uniformly: they flew above the black plastic surface for 5–30 s briefly (<1 s) touching the surface 2 to 52 times (touching flight). The tabanids landed on the test surface either directly, or performing the typical touching flight prior to landing. After landing, the insects spent at least 2 s on the test surface, where they walked randomly, during which they flew up, then landed again after about 1 s at another site of the test surface. Finally, the tabanids left the surface.

Considering any measured parameter in the first and second experiments, the shiny black plastic sheet was statistically significantly more attractive than any other test material (Tables 1 and 2): 77.8–91.3% of total landings ($\sum N_{\mathrm{I}}$) happened on the black plastic. After landing, tabanids spent 88.1–94.0% of their total time ($\sum t$) on the black plastic. On the black plastic the average period τ spent by individuals was 1.5–9.2 times of that spent on the other materials. 62.9–67.7% of the total number $\sum N_{\mathrm{F}}$ of flying-up events, and 97.4–99.4% of the total number $\sum N_{\mathrm{T}}$ of touchings were observed on the black plastic. Touching did not occur on the matt white cloth ($\sum N_{\mathrm{T}}$=0). The touching flight of tabanids was typical almost exclusively to the shiny black plastic sheet. This is the reason why the number $\sum N_{\mathrm{T}}$ of touching was so high for the shiny black plastic and so small for the other test surfaces (Tables 1 and 2).

In the second experiment no tabanid fly contacted (touched, or landed on) the black and white plastic sheets when they were vertical. However, when both test surfaces became horizontal (hourly), the same reactions of tabanids were observed (Table 2) as in the first experiment (Table 1). This was repeated three times between 9 and 14 h. In the second experiment when both test surfaces were horizontal the black plastic sheet was again statistically significantly more attractive than the white plastic sheet. No tabanids were attracted to the person, who conducted the choice experiments.

In the third experiment tabanids were attracted only to the upward-facing horizontal sticky shiny black surface laid onto the ground (number of tabanids trapped, N=45). Upward or downward-facing horizontal and vertical sticky shiny white surfaces and vertical or downward-facing sticky shiny black surfaces were unattractive (N=0) to tabanids. From this we conclude that tabanids are attracted to horizontally polarized light, if it stimulates their ventral eye region.

In the fourth experiment the flying tabanids touched the water surface one or two times only in the black water-filled tray. Since the black water-filled tray reflected highly and horizontally polarized light, while the white water-filled tray reflected very weakly and not horizontally polarized light, the results of the fourth experiment support again our main conclusion that tabanids are attracted to highly and horizontally polarized light stimulating their ventral eye region.

According to Table 3, overall the black oil-filled trays used in the fifth experiment trapped 802 tabanids, while the white ones only 25. Hence the black oil surface was 32 times more attractive to tabanids than the white one, which is again a statistically significant difference. Considering the total numbers of captured individuals, the female/male ratio was 504/298=1.7 and 15/10=1.5 in the black and white trays, respectively, but this ratio differed slightly from site to site and was also species-specific. The attraction of the black tray to *Atylotus loewianus*, *Heptatoma pellucens*, *Tabanus bovinus*, *T. bromius*, *T. exclusus*, *T. maculicornis*, *T. sudeticus*, and *T. tergestinus* was statistically significantly higher than that of the white one. In the case of several other species only a few (1–4) individuals were captured (mainly in the black tray), so that these results cannot be evaluated statistically. Hence, according to Table 3, many tabanid species preferred the highly and horizontally polarizing black oil surface against the weakly and not always horizontally polarizing white one. Thus the results of the fifth experiment support again our main conclusion that the investigated tabanids are attracted to highly and horizontally polarized light stimulating their ventral eye region.

Discussion

In the first and second experiments only the black plastic sheet reflected highly and horizontally polarized light, the other four test surfaces reflected unpolarized or weakly/moderately and not always horizontally polarized light. Since the black plastic was much more attractive than the matt black cloth, negative phototaxis (i.e. attraction to dark places), cannot explain our findings. Because the shiny black plastic sheet (reflecting a large amount of light if the angle of reflection relative to the surface is small) was significantly more attractive than the white plastic, the matt white cloth and the aluminum foil (all three surfaces reflecting a large amount of light, independently of the angle of reflection), the results can also not be explained by positive phototaxis (i.e. attraction to bright places). The temperature of the test surfaces was the same (because they were always shady), thus the preference of the black plastic by tabanids cannot be explained by temperature differences. Our test surfaces were colorless (white or black or metallic white), consequently, in our first and second experiments the color could not play an important role in the choice of tabanids.

For humans the test surfaces used in our experiments were odorless. Although it cannot be excluded that some odor differences between these dry test materials could be sensed by tabanids, our double-choice experiments with the sticky surfaces lubricated by the same glue (third experiment), and with the white and black trays filled by clean water (fourth experiment) or salad oil (fifth experiment) of the same odor show that smell could not play an important role in the attraction of tabanids to horizontal shiny black reflecting surfaces.

We thus conclude that in the first and second experiments the tabanids were attracted to the horizontal shiny black plastic sheet by the strong and horizontal polarization of reflected light. Hence these tabanids possess positive polarotaxis. If the black plastic was horizontal, it was very attractive to tabanids, while when it was vertical, it lost its attractiveness, and no tabanids were lured to it. The reason for this was that seen from above or from the side (from which flying tabanids could approach) the vertical black plastic sheet reflected obliquely or vertically polarized light, which is unattractive to polarotactic tabanids.

The eyes of many insects, in all probability also of tabanids, are regionally specialized, and thus in our second experiment it would have been important to present the optical stimuli reflected from the test surfaces in the same area of the visual field of tabanids. In our first, fourth and fifth experiments this prerequisite was satisfied, because the light reflected from the test surfaces on the ground stimulated always the ventral eye region of the approaching tabanids. Since in the second experiment the vertical plastic sheets were unattractive, we can conclude that the investigated tabanids are not attracted to linearly polarized light if it stimulates the lateral or frontal eye region. In the third experiment we checked also an elevated, downward-facing, horizontal shiny black surface to see whether tabanids were attracted to polarized light seen by their dorsal eye regions. It turned out that tabanids were not attracted to the horizontal shiny black reflecting surface hanging at a height of 190 cm. On the basis of our results we predict that retinula cells in the ventral eye region of tabanids possess rhabdoms with uniform alignment of microvilli (without rhabdomere twist), furthermore similar anatomical and physiological specializations as found in the backswimmer, *Notonecta glauca,* for example (Schwind 1985).

Although Burakova and Mazokhin-Porshnyakov (1982) studied the ultrastructure of the compound eye in the tabanid species *Haematopota pluvialis*, they did not investigate the ventral eye region. Smith and Butler (1991) studied the ultrastructure of the retina of female tabanid flies of 14 different species (*Agkistrocerus jinitimus*, *Chrysops pikei*, *C. vittatus*, *Diachlorus ferrugatus*, *Hybomitra hinei wrighti*, *Tabanus aar*, *T. atratus*, *T. gracilis*, *T. imitans*, *T. lineoia*, *T. longiusculus*, *T. molestus*, *T. petiolatus*, *T. rufojiiater*). They investigated five ommatidia from the equatorial eye region, and one dorsal ommatidium near the eye margin. They found closely spaced rhabdomeres in the distal retina and twisting of the peripheral rhabdomeres R1-R6 only in the proximal half of the ommatidium, while the central rhabdomeres R7 and R8 do not twist, and their microvilli are orthogonal to each other. From these they hypothesized that "unlike other flies, the dorsal margin of tabanid eyes may not be specialized for polarized light detection, but instead horse flies and deer flies may have some polarization sensitivity across the entire eye." Although there is no overlapping among the tabanid species studied by Smith and Butler (1991) and those investigated by us, the validity of the cited hypothesis is supported by our finding that the tabanids investigated in this work have ventral polarization vision and positive polarotaxis. The lack of information on the ultrastructure of the ventral retina in tabanid flies warrants further anatomical and electrophysiological studies of the polarization-sensitive ventral eye region in tabanids.

Behavioral experiments with *Hybomitra hinei wrighti* performed by Smith and Butler (1991) indicated that males of this species may use polarized light for orientation during mating flights: males, exhibiting mating flights only during times when direct sunlight is available, changed their direction of hovering orientation when a linearly polarizing filter was positioned over them and rotated.

Hansruedi Wildermuth (Rüti, Switzerland, personal communication, 2008) observed similar reactions to the ones we report here of *Tabanus* spp. to horizontal black plastic and dark brown perspex sheets during field experiments designed for the examination of dragonfly responses to shiny surfaces (Wildermuth 1998).

Our discovery that tabanids are attracted to horizontally polarized light stimulating their ventral eye region is remarkable for three reasons: (1) positive polarotaxis has so far only been demonstrated in aquatic insects (including water beetles and bugs, dragonflies, mayflies, and caddis flies) ovipositing directly into water (Schwind 1991, 1995; Wildermuth 1998, 2007; Horváth et al. 1998; Kriska et al. 1998, 2006, 2007, 2008; Horváth and Varjú 2004; Csabai et al. 2006), but not in insects like tabanid flies. (2) This is the first time that ventral polarization vision has been demonstrated in flies (Diptera). (3) The fact that we have shown this response to occur in a blood-sucking insect group, opens up opportunities for the design of new kinds of traps.

Since the tabanids studied do not oviposit directly into water, the question arises: what is the function of their positive polarotaxis? We propose that ventral polarization vision in tabanids has adaptive significance in four biological contexts: (1) it may provide females with an increased probability of finding hosts, because social herbivores regularly visit bodies of freshwater. (2) It will attract females to potential egg-laying sites, from which larvae can descend into water or moist mud. (3) It can guide both males and females to water bodies, which they need for drinking and temperature control. (4) It can guide males to locations where the probability of encountering females is high.

The discovery of positive polarotaxis in both sexes of tabanids offers a new method for trapping these economically important insects. The existing tabanid traps attract flies by odors (e.g., carbon dioxide, ammonia, or acetone) and/or the intensity and/or the color of reflected light (e.g., Malaise 1937; Gressitt and Gressitt 1962; Catts 1970; von Kniepert 1979; Hribar et al. 1992; Moore et al. 1996; Mihok 2002). The improvement of tabanid traps is of great practical importance in regions, especially in the tropics, where tabanids transmit dangerous diseases, because these insects cannot be exterminated by traditional methods using toxic sprays, for example. Numerous painful bites from large tabanid populations can reduce milk production from dairy and beef cattle and interfere with grazing of cattle and horses, because animals under attack will herd together (Majer 1988; personal observations, 2008). On the basis of our results presented here, the design, construction, and testing of some new effective polarizing tabanid traps are in progress.

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