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POLAROTAXIS IN TABANID FLIES AND ITS PRACTICAL SIGNIFICANCE

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A BÖGÖLYÖK POLAROTAXISA ÉS GYAKORLATI JELENTŐSÉGE

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ABSTRACT: We present here experimental evidence for the positive polarotaxis of both males and females in numerous tabanid fly species. Our results show that in these tabanids the recognition of rendezvous and oviposition sites near water bodies happens indirectly by means of the detection of horizontally polarized water-reflected light. Tabanid females usually lay their eggs on marsh-plants next to water, or mud, and after egg hatching the larvae drop down directly into water, or onto wet soil. Polarotaxis has been described earlier only in connection with the direct detection of water. Tabanids should also find water, because they need water for drinking, furthermore the surrounding of waters can be an ideal rendezvous and oviposition site for tabanids. A further particularity of our findings is that in the order Diptera the investigated tabanids are the first known species possessing ventral polarization vision. The discovery of polarotaxis in tabanids makes it possible to develop new optically luring traps being more efficient than the existing traps based on the attraction of tabanids by the brightness and/or colour of reflected light. The improvement of tabanid traps is of particular 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.

KIVONAT: Terepi választásos kísérletekkel bizonyítottuk több bögölyfaj esetében, hogy a nőstény és hím egyedeik erőteljesen vonzódnak a vízszintesen poláros fényhez, amit összetett szemük hasoldali részével érzékelnek. Terepkísérleteink során azt tapasztaltuk, hogy a vízszintesen poláros fény szupernormális ingerként hat, azaz szinte minden más ingert legyőző, ellenállhatatlan vonzerőt gyakorol a böglyökre, még akkor is, ha számos ló és/vagy szarvasmarha volt a közelükben. Mivel ezen erőteljes pozitív polarotaxis nemcsak a nőstény, hanem a hím böglyöknél is megjelenik, e reakciót nem lehet pusztán a vízhez vagy nedves talajhoz közeli petézőhely fénypolarizáció alapú keresésével magyarázni. Különböző helyszíneken folytatott terepkísérletekkel sikerült valószínűsítenünk a böglyök pozitív polarotaxisának a peterakáson túli további lehetséges funkcióit: a böglyök, sok más repülő rovarhoz hasonlóan, előszeretettel keresik föl a vizeket ivás céljából, és a legtöbb bögölyfaj vonzódik a nedves, párás helyekhez. A hím böglyök polarotaktikus vízdetekciója ugyancsak előnyös, mert ők a polarotaxissal vízhez vonzott nőstény böglyökkel találkozhatnak, s párosodhatnak. A böglyök általunk fölfedezett pozitív polarotaxisának egyik gyakorlati alkalmazásaként új típusú, fénypolarizációs bögölycsapdák fejleszthetők ki, melyek hatékony védekezést jelenthetnek az egyes területeken az emberre és haszonállatra egyaránt veszélyes kórokozókat terjesztő bögölyökkel szemben.

Key words: Diptera, Tabanidae, tabanid flies, water detection, polarization vision, positive polarotaxis, tabanid traps

Introduction

The tabanid flies (Diptera: Tabanidae) are spread world wide. Adult tabanids feed on pollen and nectar, and the females usually feed on blood. Since the females feed also on the blood of domestic animals (e.g. cattle, horse, mule, hog, dog) and even humans, the biology and behaviour of tabanids were intensely studied in the last decades (e.g. TASHIRO and Schwardt, 1953; HAYAKAWA, 1980; MAJER, 1988; HALL et al., 1998; SASAKI, 2001).

Many species of tabanids are known to play important roles in spreading diseases of livestock and other animals (KRISNSKY, 1976). In addition, several species in three or four genera are medically important to humans. The mouthparts of female tabanids are modified into the equivalent of miniature scalpels or steak knives ideal for macerating the skin to the depth of the superficial dermal vessels. A pool of blood collects in the tissues and is lapped up by the tongue-like component of the mouthparts. The bite of tabanids is quite painful but often leads to little more than a transient wheal and flare reaction with minimal bleeding from the wound. Occasionally secondary bacterial infection is a problem. Some individuals have significant urticarial reactions to tabanid bites and cases of anaphylaxis have been reported in the literature (PUCCI et al., 1995; MAAT-BLEEKER and BRONSWIJK, 1995). In addition to the affects directly related to their bites, tabanids vector at least one human disease and perhaps more. The best studied human disease vectored by tabanids is loaiasis caused by the helminth, *Loa loa*, and vectored by species in the genus Chrysops. Tabanids have been suspected as vectors of human cases of tularemia (*Francisella tularensis*), and anthrax (*Bacillus anthracis*), though hard evidence is equivocal (KRISNSKY, 1976; FOIL, 1989).

Tabanid eggs are usually laid in large, layered clusters of 100-1000 on vegetation or other objects overlying water or moist soil. The larvae, which are aquatic, semi-aquatic, or terrestrial, hatch from the eggs and drop to the water or wet soil below where they become voracious predators of other invertebrates or small vertebrates. To know how male and female tabanid flies locate their terrestrial rendezvous and egg-laying sites 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; WILSON et al., 1966; CATTS, 1970; VON KNIEPERT, 1979; WALL and DOANE, 1980; HAYAKAWA, 1980; HRIBAR et al., 1992; MOORE et al., 1996). According to ALLAN et al. (1987), the haematophagous female tabanids can find their host animals by odours, heat and visual cues. In spite of these studies, the optical cues relevant in the search for rendezvous and oviposition sites of tabanids are only poorly understood (THORSTEINSON et al., 1965; Lehane, 2005). It is a generally accepted view that size, shape, motion, brightness and colour are factors that influence the attraction of tabanids.

In this work we report on the results of our choice experiment which revealed the most important optical cue governing the remote detection of potential rendezvous and oviposition sites for tabanid flies. We present here experimental evidence for the positive polarotaxis (i.e. attraction to horizontally polarized light) of both males and females of numerous tabanid fly species. We propose that the function of polarotaxis is that tabanids detect their terrestrial rendezvous and oviposition sites near waters indirectly by means of the horizontally polarized water-reflected light. Positive polarotaxis has been described earlier only in connection with the direct visual detection of water or moist substrata (SCHWIND, 1991; HORVÁTH and VARJÚ, 2004). A further particularity of our findings is that in the order Diptera these tabanids are the first known species possessing ventral polarization vision and definite polarization-sensitive behaviour with a known function.

Materials and Methods

In the double-choice experiments, conducted for two days at four different Hungarian places (Erdőkertes, Pécsely, Kiskunhalas, Balatonszemes) being typical biotopes of tabanids, one black and one white plastic tray with a diameter of 70 cm was laid horizontally onto the grassy ground which was either shady or sunny during the day. Both trays were filled by light yellow salad oil with a height of 4 cm. According to our earlier experience, the salad oil can trap all insects that touch its surface (HORVÁTH et al., 1998; HORVÁTH and VARJÚ, 2004). The distance between the two oil-filled trays was 2 m, and their positions were transposed in every two hours from sunrise to sunset. Since tabanids fly only at daytime, between sunset and sunrise both trays were covered with a wooden board to avoid trapping of night-active insects. The trapped insects were conserved in alcohol and determined later in the laboratory. The geographical coordinates (latitude, longitude) and dates of these experiments are given in Table 1.

The reflection-polarization characteristics of the salad-oil-filled trays 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. The polarimeter's elevation was approximately equal to the Brewster's angle θ_B = 36.9° and 33.7° of the water (with refractive index n = 1.33) and plastic or salad oil ($n \approx 1.50$) surface, respectively, where θ_B = arc tan (1/n) relative to the horizon. In the case of a given non-metallic (dielectric) material, the degree of linear polarization p of reflected light is highest at the Brewster's angle, for which the light component reflected from the outer surface is completely polarized with direction of polarization parallel to the surface. When characterizing the average $p \pm$ standard deviation Δp of light reflected from a given test surface in this work, we always refer to the p-value measured at -35° from the horizontal. The reason for Δp is that due to the relatively wide field of view (50° horizontally and 40° vertically) of our videopolarimeter p changed because of the varying direction of reflection relative to the horizontal.

Results

In our choice experiment the salad oil could trap all insects touching its surface, consequently, all attracted and entrapped tabanids could be later identified.

Table 1 shows the species, number and sex of the tabanids trapped by the black and white oil-filled trays in the choice experiments performed at four different sites. As total, the black trays trapped 776 tabanids, while the white ones only 25. Hence the black oil surface was 31 times more attractive to tabanids than the white one, which is an evidently high difference. Considering the total numbers of captured individuals, the female : male ratio was 496 : 280 = 1.8 and 15 : 10 = 1.5 in the black and white trays, respectively. This ratio changed 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 obviously higher than that of the white one. In the case of several other species only a few (1-4) individuals were captured (Table 1), thus these results cannot be evaluated statistically. Hence, according to Table 1, the mentioned 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 experiments support our main conclusion that the investigated tabanids are attracted to highly and horizontally polarized light stimulating the ventral eye region.

Since all the test surfaces used in our choice experiments were practically colourless, their reflection-polarization characteristics were practically independent of the wavelength of light. The salad-oil-filled black trays reflected horizontally polarized light with high p-values (p = 70% ± 20% = average ± standard deviation). The salad-oil-filled white trays reflected vertically or obliquely polarized light with very low p-values (p = 10% ± 10%) or unpolarized light (p = 0%).

Table 1. Species, number and sex (f: female, m: male) of the tabanid flies trapped by the black and white trays filled with salad oil in our choice experiments performed at four different sites, the geographic coordinates (latitude, longitude) of which are also given together with the dates of the experiments.

site, latitude, longitude, date (2007)	tabanid species	oil-filled tray: black	oil-filled tray: white
Erdőkertes 47° 40' N, 19° 19' E, 8-9 July	*Atylotus fulvus*	f = 0, m = 1	f = 0, m = 0
	Chrysops caecutiens	f = 0, m = 0	f = 0, m = 1
	Chrysops divaricatius	f = 0, m = 1	f = 0, m = 0
	Chrysosps viduatus	f = 1, m = 1	f = 0, m = 0
	Chrysops sp.	f = 0, m = 1	f = 0, m = 0
	Hybomitra acuminata	f = 1, m = 1	f = 0, m = 0
	Hybomitra lundbecki	f = 0, m = 1	f = 0, m = 0
	Hybomitra nitidifrons confusa	f = 0, m = 1	f = 0, m = 0
	Heptatoma pellucens	f = 2, m = 4	f = 0, m = 0
	Haematopota pluvialis	f = 1, m = 0	f = 0, m = 0
	Hybomitra tropica	f = 1, m = 0	f = 0, m = 0
	Tabanus bovinus	f = 17, m = 3	f = 0, m = 0
	Tabanus bromius	f = 69, m = 22	f = 3, m = 3
	Tabanus cordiger	f = 0, m = 1	f = 0, m = 0
	Tabanus exclusus	f = 8, m = 2	f = 0, m = 0
	Tabanus glaucopis	f = 1, m = 3	f = 0, m = 0
	Tabanus maculicomis	f = 116, m = 23	f = 0, m = 0
	Tabanus spectabilis	f = 0, m = 1	f = 0, m = 0
	Tabanus sudeticus	f = 0, m = 1	f = 0, m = 0
	Tabanus tergestinus	f = 173, m = 173	f = 7, m = 2
	Tabanus unifastiatus	f = 2, m = 1	f = 0, m = 0
	sum	**f = 392, m = 241**	**f = 10, m = 6**
Pécsely 46° 57' N, 17° 47' E, 20-21 July	*Atylotus fulvus*	f = 4, m = 0	f = 0, m = 0
	Atylotus loewianus	f = 3, m = 2	f = 0, m = 0
	Atylotus sp.	f = 1, m = 2	f = 0, m = 0
	Tabanus bromius	f = 22, m = 5	f = 0, m = 0
	Tabanus bifarius	f = 1, m = 0	f = 0, m = 0
	Tabanus maculicomis	f = 3, m = 4	f = 3, m = 2
	Tabanus miki	f = 1, m = 0	f = 0, m = 0
	Tabanus tergestinus	f = 9, m = 5	f = 1, m = 0
	Tabanus sudeticus	f = 3, m = 2	f = 0, m = 0
	sum	**f = 47, m = 20**	**f = 4, m = 2**
Kiskunhalas 46° 43' N, 19° 5' E, 28-29 June	*Chrysosps viduatus*	f = 2, m = 2	f = 0, m = 0
	Tabanus bromius	f = 25, m = 3	f = 0, m = 2
	Tabanus cordiger	f = 0, m = 1	f = 0, m = 0
	Tabanus glaucopis	f = 0, m = 1	f = 0, m = 0
	Tabanus maculicomis	f = 12, m = 1	f = 0, m = 0
	Tabanus sudeticus	f = 2, m = 5	f = 0, m = 0
	Tabanus tergestinus	f = 4, m = 2	f = 1, m = 0
	sum	**f = 45, m = 15**	**f = 1, m = 2**
Balatonszemes 46° 49' N, 17° 47' E, 16-17 July	*Chrysosps viduatus*	f = 3, m = 0	f = 0, m = 0
	Tabanus bromius	f = 0, m = 1	f = 0, m = 0
	Tabanus cordiger	f = 0, m = 2	f = 0, m = 0
	Tabanus maculicomis	f = 1, m = 0	f = 0, m = 0
	Tabanus spodoptemus	f = 1, m = 0	f = 0, m = 0
	Tabanus sudeticus	f = 0, m = 1	f = 0, m = 0
	Tabanus tergestinus	f = 7, m = 0	f = 0, m = 0
	sum	**f = 12, m = 4**	**f = 0, m = 0**
	total	**f = 496, m = 280**	**f = 15, m = 10**

Discussion and Conclusion

The main intention of this work was to demonstrate behaviourally the ventral polarization vision manifesting in positive polarotaxis (i.e. attraction to horizontally polarized light) in numerous tabanid species, and the efficiency of the salad-oil-filled black tray functioning as a tabanid trap.

In the choice experiments our test surfaces were colourless (white or black) for the human eye. Consequently, in these experiments the colour could not play an important role in the choice of tabanids. Our experiments with the white and black trays filled with salad oil of the same odour show that the smell could not play an important role in the attraction of tabanids by horizontal black reflecting surfaces. In our experiments the light reflected from the test surfaces laid on the ground stimulated always the ventral eye region of the approaching tabanids.

The fact that no tabanids attacked the persons (observers) conducting the choice experiments shows that the tabanids attracted to the highly and horizontally polarizing test surfaces might not look for potential blood hosts. It has long been recognized that carbon dioxide is a strong attractant for host-seeking tabanids (WILSON et al., 1966; LEHANE, 2005). Because of the similarity of the optical stimulus between our highly and horizontally polarizing test surfaces and dark water surfaces the interpretation, that the attracted tabanids were probably searching for water puddles in order to take up moisture, seems to be feasible.

Our discovery that tabanids are attracted to horizontally polarized light is remarkable for three reasons:

(1) The observed tabanids do not lay their eggs directly into water, but they oviposit onto marsh-plants, from which the hatched larvae can drop into water or onto mud. Until now, attraction by horizontally polarized light has been found only in aquatic beetles, water bugs, dragonflies and mayflies, which oviposit directly into water (SCHWIND, 1991; WILDERMUTH, 1998; HORVÁTH et al., 1998; KRISKA et al. 1998, 2006; HORVÁTH and VARJÚ, 2004; CSABAI et al., 2006).

(2) Tabanids belong to the order Diptera, and earlier no any dipteran species has been found that would be attracted by horizontally polarized light. Ventral polarization vision with definite polarization-sensitive behaviour of known functions has not been demonstrated in dipterans.

(3) Among blood-sucking insects (LEHANE, 2005) tabanids are the first animal group in which ventral polarization vision and positive polarotaxis are evidenced, which can be used to design new polarized light traps.

Many tabanid species lay their egg batches on the lower side of leaves leaning above water or mud (HAYAKAWA, 1980; MAJER, 1988). After egg hatching the tabanid larvae drop into water or onto wet soil. Thus, on the basis of our results presented here we propose that one of the functions of polarotaxis in tabanids is that the females first recognize remotely the water surface by means of the horizontally polarized water-reflected light, and only then look for plants near water as possible egg-laying sites. Male tabanids should also find water, because tabanid females can be found with a high probability on the shore of water bodies due to the mentioned reasons. Of course, both male and female tabanids need water for drinking (JONES, 1922; HAYAKAWA, 1980; personal observations). Thus, positive polarotaxis makes possible the direct remote detection of water for drinking, and the indirect remote recognition of rendezvous and oviposition sites for tabanids. Note that the latter are quite new functions of polarotaxis: polarotaxis has been described earlier only in connection with the direct visual detection of water in aquatic insects (SCHWIND, 1991; HORVÁTH and VARJÚ, 2004).

According to Table 1, in our experiment the black oil-filled trays trapped always (1.6-3.0 times) more female tabanids than males. This more or less skewed sex-ratio may be the result of the sex-specific capturing efficiency of the oil-filled traps used. Note that the behaviour (e.g. host-seeking, egg-laying, oviposition site selection) of female tabanids is different from that of males. One could also imagine that the males are mainly elsewhere and mating occurs also elsewhere, or the males are not attracted to water in the same extent as females are, because only females lay eggs onto the plants near waters (Lehane, 2005).

The discovery of positive polarotaxis in both sexes of tabanids offers a new method for trapping tabanids, especially males being underrepresented in many existing tabanid traps (HALL et al, 1998). These new traps will use different optically luring components, which produce highly and horizontally polarized light. The existing tabanid traps attract flies by odours and/or the intensity and/or the colour of reflected light, rather than by polarized light (GRESSITT and GRESSITT, 1962; WILSON et al., 1966; VON KNIEPERT, 1979; HRIBAR et al., 1992; MOORE et al., 1996; SASAKI, 2001). Traps with a strong visually luring component include the 'canopy trap' (CATTS, 1970), 'Manitoba trap' (THORSTEINSON et al., 1965) and 'box trap' (WALL and DOANE, 1980). The 'Malaise trap' (MALAISE, 1937) and the 'Nzi trap' (MIHOK, 2002) can catch tabanids by simply being in their flight paths, or by the use of attractants, such as carbon dioxide, ammonia or acetone, for example. On the basis of our results the design, construction and testing of some new effective polarizing tabanid traps are in progress.

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