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A new tabanid trap applying a modified concept of the old flypaper: Linearly polarising sticky black surfaces as an effective tool to catch polarotactic horseflies

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ABSTRACT

Trapping flies with sticky paper sheets is an ancient method. The classic flypaper has four typical characteristics: (i) its sticky paper is bright (chamois, light yellow or white), (ii) it is strip-shaped, (iii) it hangs vertically, and (iv) it is positioned high (several metres) above ground level. Such flypapers, however, do not trap horseflies (tabanids). There is a great need to kill horseflies with efficient traps because they are vectors of dangerous diseases, and due to their continuous annoyance livestock cannot graze, horses cannot be ridden, and meat and milk production from cattle is drastically reduced. Based on earlier findings on the positive polarotaxis (attraction to linearly polarised light) in tabanid flies and modifying the concept of the old flypaper, we constructed a new horsefly trap called "horseflypaper". In four field experiments we showed that the ideal horseflypaper (i) is shiny black, (ii) has an appropriately large (75×75 cm^2) surface area, (iii) has sticky black vertical and horizontal surfaces in an L-shaped arrangement, and (iv) its horizontal surface should be at ground level for maximum effectiveness. Using imaging polarimetry, we measured the reflection-polarisation characteristics of this new polarisation tabanid trap. The ideal optical and geometrical characteristics of this trap revealed in field experiments are also explained. The horizontal part of the trap captures water-seeking male and female tabanids, while the vertical part catches host-seeking female tabanids.

1. Introduction

It is a well-known fact that certain flies can be trapped by a sticky paper strip hanging vertically from the ceiling. This ancient trap is called "flypaper" and has been used from the beginning of the history of mankind (Beavis, 1988). Several different types of such flytraps are used to catch various insect species/groups for scientific purposes (Jactel et al., 2006; Kamarudin and Arshad, 2006; Chadee and Ritchie, 2010; Faiman et al., 2011), or for practical reasons in agriculture (Coli et al., 1985; Stejskal, 1995; Cross et al., 2006; Moreau and Isman, 2012). Depending on their application, the material (paper or plastic), colour, shape (e.g. rectangular or circular), stickiness (more or less tacky), alignment (vertical, tilted or horizontal) and position (e.g. laid on the ground, on an elevated substrate or hanging high in the air) of these flytraps differ. Classic flypapers possess four typical characteristics: (i) their sticky paper is usually bright (chamois, light yellow or white), (ii) their shape is a strip, (iii) they hang vertically in the air, and (iv) they are positioned several metres above the ground so they will not disturb people and/or animals in the vicinity.

Although these classic flypapers catch numerous different insect species, they do not trap tabanid flies. However, there is a great need to kill tabanids with effective traps because they are vectors of dangerous diseases (Foil, 1989; Luger, 1990; Hall et al., 1998; Sasaki, 2001; Lehane, 2005). Also, their continuous annoyance to livestock prevents grazing; horses cannot be ridden and meat and milk production from cattle is drastically reduced (Hunter and Moorhouse, 1976; Harris et al., 1987; Lehane, 2005). Several different trap types have been developed to reduce the number of tabanids (Malaise, 1937; Gressitt and Gressitt, 1962; Wilson et al., 1966; Catts, 1970; Roberts, 1977; von Kniepert, 1979; Hayakawa, 1980; Wall and Doane, 1980; Hribar et al., 1991, 1992; Moore et al., 1996; Mihok, 2002). There are three main kinds of conventional tabanid traps: (i) flight interception traps, (ii) chemically baited canopy traps, and (iii) optically baited canopy traps. The common feature of these traps is that they are designed to attract female tabanids visually with shiny black objects and/or

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surfaces. It is generally believed that such black structures may simulate the dark silhouette of a host animal and if they are flapping in the wind, their motion might mimic that of the host and attract female tabanids that want to suck blood (Thorsteinson et al., 1965, 1966; Lehane, 2005). The most frequently used visual target in these traps is a shiny black ball (e.g. a simple beach ball painted black). An important aspect of the optical attraction of such a ball due to linearly (or plane) polarised reflected light was recently revealed by Egri et al. (2012a).

Tabanids have positive polarotaxis, i.e. they are attracted to linearly polarised light (Horváth et al., 2008; Egri et al., 2012a), and this polarotactic behaviour can be used to develop new tabanid traps. Recently, Blahó et al. (2012a) designed such a polarisation tabanid trap, the visual target of which is a horizontal solar panel (photovoltaics) attracting polarotactic tabanids by means of the horizontally polarised light reflected from the photovoltaic surface. The tabanids trying to touch or land on the photovoltaic trap surface are killed by the mechanical force of a wire rotated at a high speed with an electric motor powered by electricity produced by the solar panel.

The aim of this work was to describe another new tabanid trap that applies a modified concept of the old flypaper. We show here that linearly polarising vertical and horizontal sticky black surfaces is an effective tool to catch polarotactic male and female tabanid flies. In field experiments the ideal optical and geometrical characteristics of this sticky tabanid trap were determined. Using imaging polarimetry, we measured the reflection-polarisation characteristics of this trap to demonstrate the optical causes for the polarisation attraction for tabanid flies. The novel tabanid trap is a practical application of the knowledge accumulated during the last few years on polarotaxis in tabanids (Horváth et al., 2008, 2010a,b; Kriska et al., 2009; Blahó et al., 2012a,b; Egri et al., 2012a,b).

2. Materials and methods

2.1. The greyness experiment

Experiment 1 was performed between 21 June and 12 September 2012 on a Hungarian horse farm at Szokolya (47° 52′ N, 19° 00′ E), where tabanids were found in large numbers. To study the influence of the brightness of horizontal and vertical sticky traps on the attraction for tabanids, four pairs of plastic sheets ($50 \times 50 \times 0.5$ cm) were used (Fig. 1A; Supplementary Fig. S1) (any black plastic is suitable). One piece of each plastic test surface pair was horizontal, and the other piece was vertical. The first test surface pair was black, the second, third and fourth pairs were dark grey, light grey and white, respectively. The centre of each vertical test surface was fixed at a height of 100 cm from the ground between two vertical metal rods driven into the ground with a hammer. Each horizontal test surface was fixed on the ground with four L-shaped metal hooks. The test surface pairs were set up 5 m apart along a straight line. The horizontal distance was 50 cm between the horizontal and vertical pieces of each test surface pair. All eight test surfaces were simultaneously either in the sun or in the shade, and covered by a transparent, odourless, weather-proof insect-monitoring adhesive (BabolnaBio, Hungary). Periodically the tabanids trapped by these sticky test surfaces were removed and counted. The surfaces were then cleaned with petrol, the order of the test surface pairs rotated according to a pre-determined randomised plan and the adhesive reapplied. The identification to species level of the tabanids collected from these sticky surfaces was impossible because their bodies were seriously damaged. It was obvious, however, that they were tabanids (Diptera: Tabanidae). In previous field experiments (Blahó et al., 2012b; Egri et al., 2012b) the following tabanid species were found to occur at the same study site with the use of self-made liquid-filled traps applied in earlier field experiments (Horváth et al., 2008, 2010b, 2011; Kriska et al., 2009; Blahó et al., 2012a,b; Egri et al., 2012a,b): *Tabanus tergestinus*, *Tabanus bromius*, *Tabanus bovinus*, *Tabanus autumnalis*, *Atylotus fulvus*, *Atylotus loewianus*, *Atylotus rusticus*, *Haematopota italica*.

2.2. Height experiment

Experiment 2 was performed between 21 June and 12 September 2012 at a distance of 100 m from the site of Experiment 1. To study the influence of height on horizontal and vertical sticky test surfaces in the attraction for tabanids, four pairs of black plastic sheets ($50 \times 50 \times 0.5$ cm) were used (Fig. 1B; Supplementary Fig. S2) (any black plastic is suitable). One piece of each test surface pair was horizontal, while the other piece was vertical. The first pair was set on the ground, while the second, third and fourth pairs were set at heights of 50, 100 and 150 cm from ground level, respectively (these values refer to the height of the plane of the horizontal test surfaces and of the lower edge of the vertical test surfaces). Each elevated horizontal test surface was fixed to four vertical metal rods driven into the ground with a hammer. The horizontal test surfaces were fixed on the ground with four L-shaped metal hooks. The tabanids trapped by these sticky black test surfaces were periodically counted. Other details of this experiment were the same as for Experiment 1.

2.3. Size experiment

Experiment 3 was performed between 21 June and 12 September 2012 at a distance of 100 m from the site of Experiment 2. To study the influence of the size of horizontal and vertical sticky black test surfaces on the attraction for tabanids, four pairs of black plastic sheets were used (Fig. 1C; Supplementary Fig. S3) (any black plastic is suitable). One piece of each test surface pair was laid horizontally on the ground, and the other piece was set vertically with its centre at 100 cm above ground level. The dimensions of the sticky plastic sheets (thickness = 0.5 cm) of the first, second, third and fourth test surface pairs were 25×25, 50×50, 75×75 and 100×100 cm^2, respectively. The trapped tabanids were counted frequently. Other details of this experiment were the same as those of Experiment 1.

2.4. Prototype experiment

Experiment 4 was performed between 28 July and 12 September 2012 at a distance of 100 m from the site of Experiment 3. In this experiment the functioning of a prototype of our new polarisation horseflypaper was tested (Fig. 1D, Fig. 2; Supplementary Fig. S4), the concept of which is patented in Hungary (patent number: P-07-00104, year of submission: 2007, year of publication: 2009). The prototype uses a roll of sticky insect-monitoring plastic foil (Rentokil FE-217 Luminos, width = 37 cm with a central 30 cm wide sticky band on one side). It has a wooden base plate (43×57 cm^2) painted shiny black. On one short side of this base plate, two perpendicular holders are mounted that have symmetrical engravings so that they can hold the roll of sticky foil. The foil should be rolled out, with the sticky side facing up, along the base plate until it covers the whole plate. Then the sticky foil is fixed with four screws, along its two non-sticky long margins, through two black wooden battens to the base plate. We used two optional supporting sticks that can be mounted to the prototype in such a way that the sticky foil stands vertically instead of horizontally so that the tabanid-capturing effectiveness of the trap for both orientations can be measured. The whole trap made of wooden boards and battens was painted shiny black to maximise the

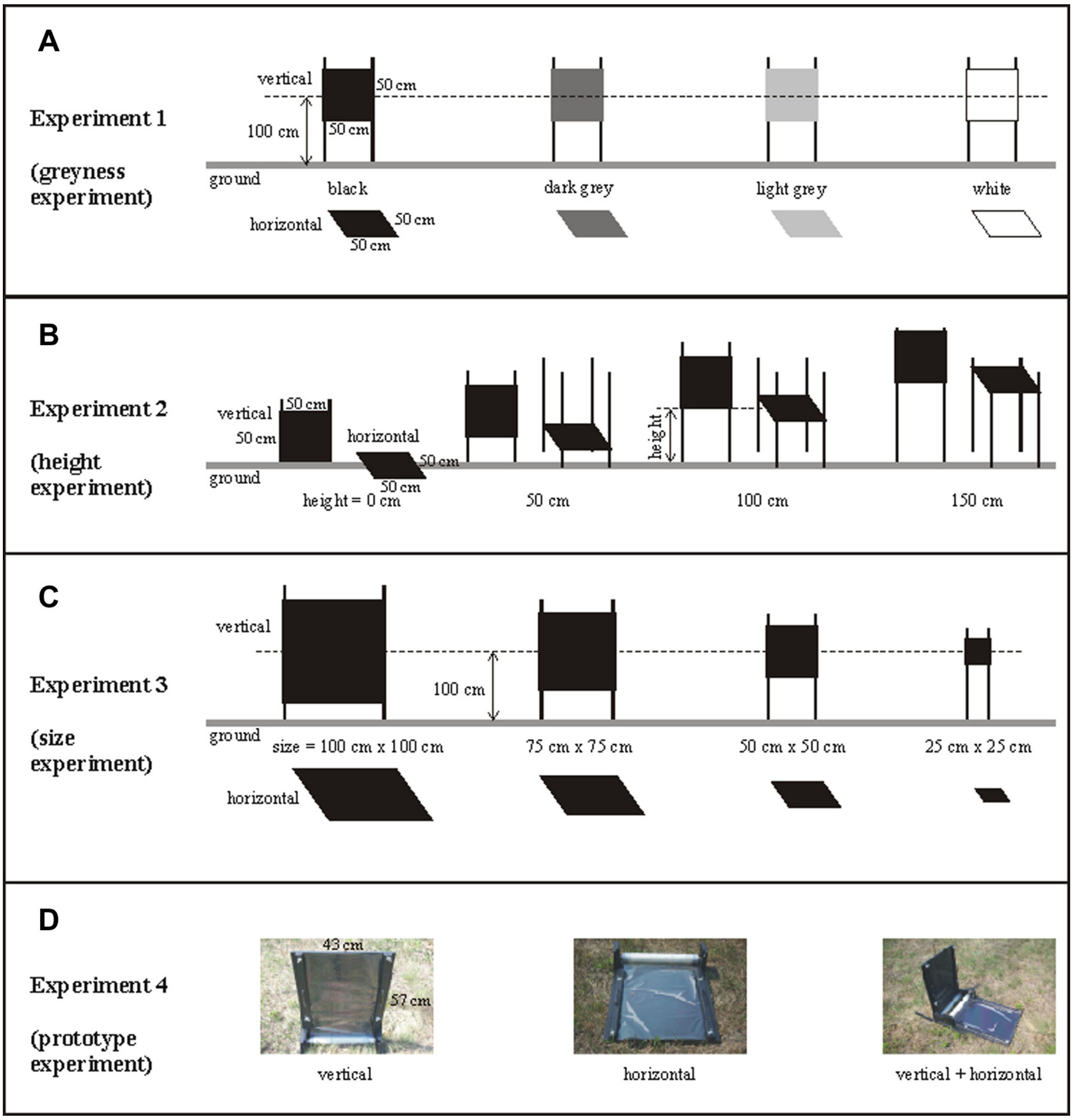

Fig. 1. Arrangements of the different sticky tabanid traps used in four field experiments studying the influence of greyness (A), height (B), size (C) and alignment (D) of trap surfaces on the tabanid-capturing efficacy.

degree of polarisation of trap-reflected light. Three different trap arrangements were used: (i) one vertical sticky black plate standing on the ground, (ii) one horizontal sticky black plate laid on the ground, (iii) an L-shaped pair with a vertical and a horizontal sticky black plate on the ground. These three traps were on the ground 5 m apart along a straight line (Figs. 1D and 2). The trapped tabanids were counted periodically. Other details of this experiment were the same as those of Experiment 1.

2.5. Duration and repetition of experiments

In all four experiments sticky visual targets with different reflection-polarisation characteristics were used to capture tabanids, which were frequently counted and removed, then the order of the test surfaces was randomly changed from a pre-determined plan. Our counting periods varied in periodicity. The slight non-uniformity of these periods was purposive: after cool, rainy and windy weather the counting period was longer with a few days to compensate for the decrease in tabanid flight activity. Because the trapped tabanids and all other insects were removed by frequent cleaning of the sticky test surfaces with petrol and the adhesive was reapplied, the newly arrived tabanids were not influenced by the presence of other trapped insects. Thus, the altered situation after each tabanid counting represented a new replication of a given experiment. In our experiments the number R of replications during a test period composed of number of days D were as follows: Experiment 1: $R = 12$, $D = 84$; Experiment 2: $R = 12$, $D = 84$; Experiment 3: $R = 12$, $D = 84$; Experiment 4: $R = 7$, $D = 47$. These numbers of replications were large enough to detect statistical differences in the numbers of trapped tabanids.

2.6. Reflection-polarisation characteristics

The reflection-polarisation characteristics of the test surfaces used in the experiments were measured by a self-constructed imaging polarimeter in the red (650 ± 40 nm = wavelength of maximal sensitivity ± half bandwidth of the charge-coupled device (CCD) detectors of the polarimeter), green (550 ± 40 nm) and blue

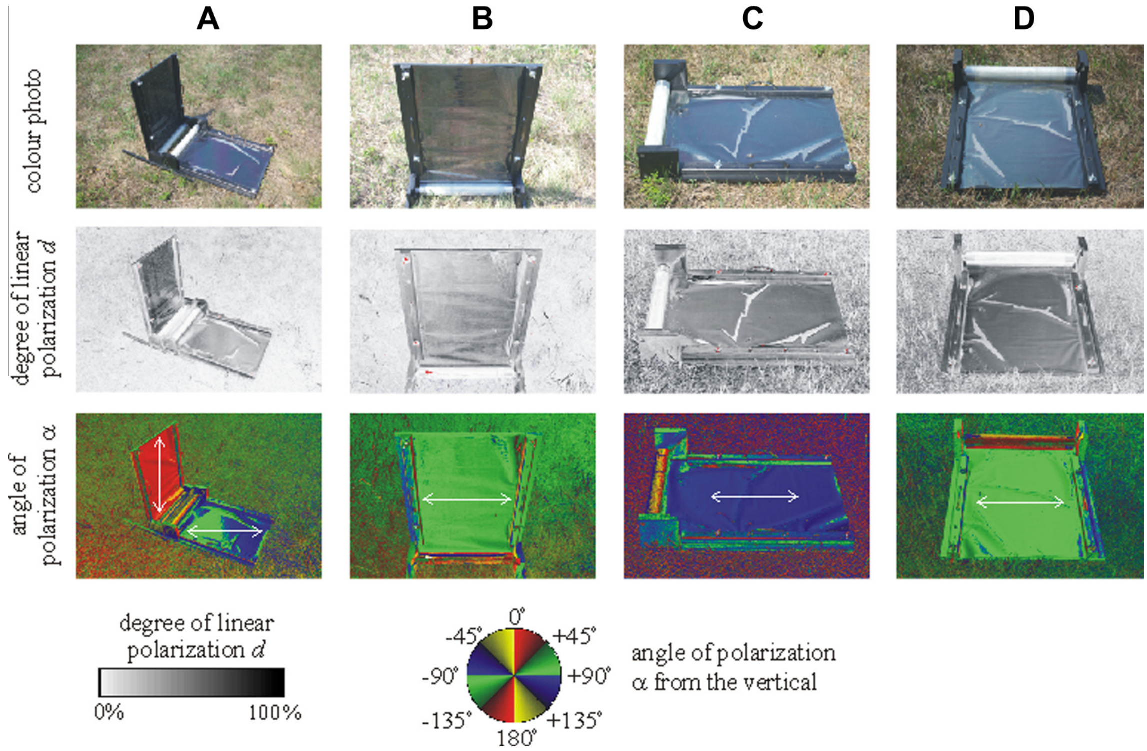

Fig. 2. Photographs and patterns of the degree of linear polarisation *d* and the angle of polarisation α (clockwise from the vertical) for the horizontal and vertical sticky black surfaces of the prototype of the new polarisation horseflypaper used in Experiment 4. Double-headed arrows show the direction of polarisation of light reflected from the trap surfaces. The patterns were measured in the blue part of the spectrum by imaging polarimetry from different directions of view relative to the trap surfaces. The traps were illuminated by direct sunlight. The angle of elevation of the optical axis of the polarimeter was −35° from the horizontal.

(450 ± 40 nm) parts of the spectrum (Figs. 2 and 3). The method of imaging polarimetry and our polarimeter have been described in detail by Horváth and Varjú (1997, 2004). Here we present only the polarisation patterns measured in the blue part of the spectrum. Practically the same patterns were obtained in the red and green spectral ranges, because the test surfaces were white, grey, or black.

2.7. Statistical analyses

The Mann–Whitney *U* tests were performed using the program Statistica 7.0.

3. Results

3.1. Test surface greyness

As shown in Table 1, in Experiment 1 the black test surfaces captured the most tabanids (horizontal: 51.2%, vertical: 54.1%), the dark grey test surfaces of the same size were slightly less attractive (horizontal: 46.8%, vertical: 34.7%), while the light grey (horizontal: 1.9%, vertical: 1%) and white (horizontal: 0.1%, vertical: 10.2%) test surfaces of the same size attracted only a few tabanids. The horizontal black, dark grey and light grey test surfaces trapped 16.7, 23.8 and 33 times more tabanids than the

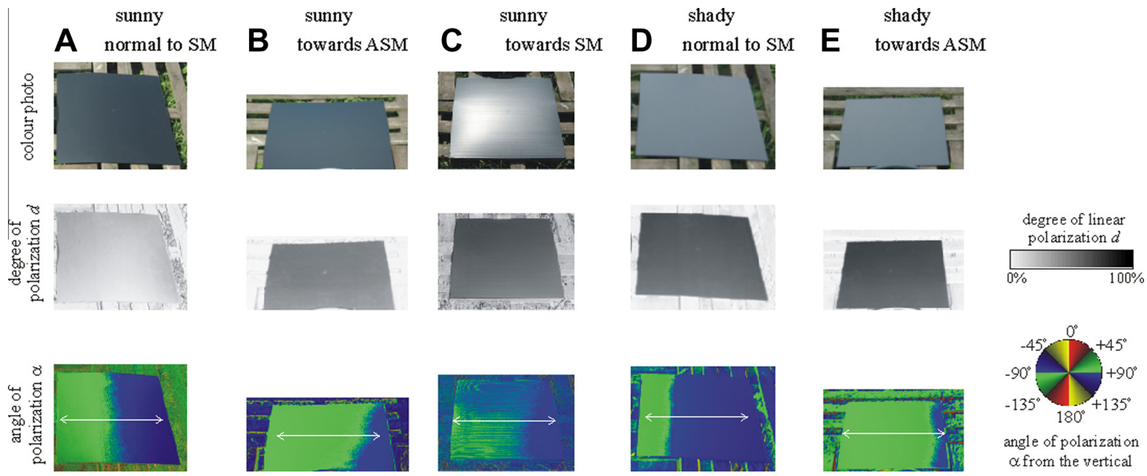

Fig. 3. Photographs and patterns of the degree of linear polarisation *d* and the angle of polarisation α (clockwise from the vertical) for a horizontal shiny black test surface measured in the blue part of the spectrum when it was sunny (A, B, C) or shady (D, E) for different directions of view relative to the solar meridian (SM). Towards SM means that the polarimeter was oriented to the solar meridian. Towards ASM means that the polarimeter faced to the anti-solar meridian. Normal to SM means that the polarimeter was oriented normal to the solar meridian. Double-headed arrows show the direction of polarisation of light reflected from the test surface. The shady test surface was illuminated by the light from a totally overcast sky. The angle of elevation of the optical axis of the polarimeter was nearly −35° from the horizontal.

Table 1
Number of tabanids captured by the horizontal and vertical sticky black, dark grey, light grey and white test surfaces of the same size in Experiment 1. The percentages given in brackets are calculated separately for the horizontal and vertical test surfaces.

Date (2012)	Horizontal sticky test surfaces				Vertical sticky test surfaces			
	Black	Dark grey	Light grey	White	Black	Dark grey	Light grey	White
28 June	85	44	1	0	12	5	0	2
1 July	16	84	1	0	11	11	0	5
10 July	280	139	26	0	24	4	1	2
17 July	141	175	0	0	2	1	0	0
25 July	141	122	1	0	2	3	0	0
28 July	1	5	0	0	1	3	0	0
8 August	37	63	0	0	0	2	0	0
15 August	42	42	1	0	0	4	0	0
23 August	96	73	0	0	0	0	0	0
29 August	30	37	0	1	0	0	0	0
4 September	16	20	3	0	0	0	0	0
12 September	1	5	0	0	1	1	0	1
Total	886 (51.2%)	809 (46.8%)	33 (1.9%)	1 (0.1%)	53 (54.1%)	34 (34.7%)	1 (1.0%)	10 (10.2%)

Table 2
Number of tabanids captured by the horizontal and vertical sticky black test surfaces positioned on the ground (0 cm) and at a height of 50, 100 and 150 cm from the ground in Experiment 2. The percentages given in brackets are calculated separately for the horizontal and vertical test surfaces.

Date (2012)	Horizontal sticky black test surfaces				Vertical sticky black test surfaces			
	0 cm	50 cm	100 cm	150 cm	0 cm	50 cm	100 cm	150 cm
28 June	162	0	0	0	8	4	5	6
1 July	39	0	0	0	2	1	18	13
10 July	428	3	0	0	5	10	29	20
17 July	234	2	0	0	0	1	1	3
25 July	136	1	0	0	2	4	2	3
28 July	13	0	1	0	1	1	0	5
8 August	25	3	2	2	3	2	0	0
15 August	93	0	0	0	1	0	2	1
23 August	136	0	0	0	0	0	1	0
29 August	40	0	0	0	0	0	1	0
4 September	15	0	0	0	0	0	0	0
12 September	29	0	0	0	0	1	0	0
Total	1,350 (98.9%)	9 (0.7%)	3 (0.2%)	2 (0.2%)	22 (14.1%)	24 (15.4%)	59 (37.8%)	51 (32.7%)

Table 3
Number (n) of tabanids captured by the horizontal and vertical sticky black test surfaces with dimensions 25 × 25 cm ($A = 0.0625$ m^2), 50 × 50 cm ($A = 0.25$ m^2), 75 × 75 cm ($A = 0.5625$ m^2) and 100 × 100 cm ($A = 1$ m^2) in Experiment 3. The numbers trapped per 1 m^2 are given in brackets. The surface density is $\delta = n/A$, where n is the total number of captured tabanids, and A is the surface area of the test surface.

Date (2012)	Horizontal sticky black test surfaces				Vertical sticky black test surfaces			
	25 × 25	50 × 50	75 × 75	100 × 100	25 × 25	50 × 50	75 × 75	100 × 100
28 June	0 (0)	53 (212)	186 (331)	319 (319)	1 (16)	4 (16)	26 (46)	27 (27)
1 July	0 (0)	8 (32)	41 (73)	68 (68)	0 (0)	5 (20)	30 (53)	30 (30)
10 July	18 (288)	265 (1,060)	578 (1,028)	987 (987)	4 (64)	11 (44)	42 (75)	70 (70)
17 July	2 (32)	113 (452)	321 (571)	515 (515)	3 (48)	11 (44)	8 (14)	20 (20)
25 July	3 (48)	89 (356)	239 (425)	407 (407)	0 (0)	0 (0)	5 (9)	14 (14)
28 July	1 (16)	7 (28)	3 (5)	9 (9)	0 (0)	0 (0)	2 (4)	2 (2)
8 August	3 (48)	50 (200)	113 (201)	328 (328)	0 (0)	2 (8)	8 (14)	18 (18)
15 August	10 (160)	86 (344)	190 (338)	297 (297)	0 (0)	0 (0)	2 (4)	3 (3)
23 August	15 (240)	76 (304)	204 (363)	342 (342)	0 (0)	0 (0)	4 (7)	4 (4)
29 August	4 (64)	26 (104)	69 (123)	100 (100)	1 (16)	1 (4)	0 (0)	4 (4)
4 September	1 (16)	8 (32)	36 (64)	58 (58)	0 (0)	0 (0)	1 (2)	0 (0)
12 September	0 (0)	1 (4)	12 (21)	17 (17)	0 (0)	2 (8)	2 (4)	4 (4)
Total (n)	57	782	1,992	3,447	9	36	130	196
Density δ (1/m^2)	912	3,128	3,541	3,447	144	144	231	196

corresponding vertical surfaces, respectively. On the other hand, the white vertical test surface trapped 10 times more tabanids than the horizontal white surface. From Experiment 1 we concluded that (i) a sticky horizontal or vertical surface captures the most tabanids if it is black or dark grey, furthermore (ii) a horizontal black sticky surface on the ground can trap more than 15 times as many tabanids as a vertical one of the same size. These two differences are statistically significant (Supplementary Table S1).

3.2. Test surface height

Table 2 shows that in Experiment 2 a horizontal sticky black test surface trapped tabanids (98.9%) only if it was on the ground. The horizontal black test surfaces of the same size at a height of 50, 100 and 150 cm captured only 0.7%, 0.2% and 0.2% of the total catches, respectively. On the other hand, the vertical sticky black test surfaces on (0 cm) and near (50 cm) the ground trapped fewer

Table 4
Number of tabanids captured by (i) the vertical sticky black surface standing on the ground, (ii) the horizontal sticky black surface laid on the ground, and (iii) the L-shaped combined sticky black trap with a vertical and a horizontal surface used in Experiment 4. The percentages given in brackets in row 'Sum' were calculated by pooling the data for all four test surfaces. The percentages given in brackets in row 'Total' were calculated separately for the pair of single vertical and horizontal surfaces, and the L-shaped combined trap.

Date (2012)	Sticky black surfaces of the new tabanid trap (horseflypaper)			
	Single vertical	Single horizontal	L-shaped combined	
			Vertical	Horizontal
31 July	3	26	5	22
8 August	11	45	4	99
15 August	5	51	0	45
23 August	1	22	5	30
29 August	4	27	5	29
4 September	3	23	5	35
12 September	1	3	2	4
Sum	28 (5.4%)	197 (38.3%)	26 (5.0%)	264 (51.3%)
Total	225 (43.7%)		290 (56.3%)	

(14.1% and 15.4%) tabanids than the more elevated (100 and 150 cm) vertical surfaces of the same size (37.8% and 32.7%). The horizontal test surface on the ground captured approximately 23 times more tabanids than the most effective vertical surface at 100 cm from the ground. From Experiment 2 we concluded that a horizontal sticky black surface captures the most tabanids if it is on the ground (Supplementary Table S2), where it traps more than 20 times as many tabanids as a vertical sticky black surface of the same size at a height of approximately 1 m above the ground.

3.3. Test surface size

From Table 3 it is clear that in Experiment 3 the number of trapped tabanids increased with the size of the sticky black test surface, independently of the surface orientation (horizontal or vertical). A horizontal test surface of a given size captured significantly (6.3, 21.7, 15.3, 17.6 times) more tabanids than the corresponding vertical test surface of the same size (Supplementary Table S3). The surface density (δ) of trapped tabanids (number of catches per 1 m^2) was maximal for both the horizontal (δ = 3,541/m^2) and the vertical (δ = 231/m^2) test surfaces with dimensions of 75 × 75 cm^2. The surface densities (δ) of catches for the two smaller (25 × 25 and 50 × 50 cm^2) vertical test surfaces were equal, while δ for the smallest (25 × 25 cm^2) horizontal test surface (δ = 912/m^2) was less than that for the second largest (50 × 50 cm^2) horizontal test surface (δ = 3,128/m^2). The differences between the δ-values for the horizontal and vertical test surfaces were, however, not statistically significant (Supplementary Table S3). From Experiment 3 we concluded that the larger a horizontal or vertical sticky black surface, the greater the number of captured tabanids (Supplementary Fig. S5), and the ideal dimensions of horizontal and vertical sticky traps are 75 × 75 cm^2 for maximum surface density of catches.

3.4. Horseflypaper prototype

In Experiment 4 (Table 4) the vertical sticky black surface of the new polarisation tabanid trap (horseflypaper) captured significantly fewer tabanids (5.4% and 5%) than the horizontal sticky black surface (38.3% and 51.3%). The horizontal surface (H_L) of the L-shaped combined trap caught more tabanids (51.3%) than the single horizontal surface (H_S) (38.3%) but this difference was not significant (Supplementary Table S4). The small difference between the catches of the vertical surfaces, V_L (combined: 5%) and V_S (single: 5.4%), was also not significant (Supplementary Table S4). The combined trap captured more tabanids ($H_L + V_L$ = 56.3%) than the single horizontal (H_S = 38.3%) and vertical (V_S = 5.4%) traps together ($H_S + V_S$ = 43.7%), but this difference was not significant (Supplementary Table S4). The horizontal trap surfaces captured 7.0 and 10.2 times more tabanids than the vertical ones, which are statistically significant differences (Supplementary Table S4). From Experiment 4 we concluded that the prototype of our new polarisation tabanid trap functions excellently under field conditions (Figs. 1D and 2; Supplementary Fig. S4), and it is worthwhile combining both the vertical and the horizontal sticky black trap surfaces in an L-shaped arrangement to maximise tabanid catches. Due to practical reasons, the vertical part of the new trap stood on the ground, since it would be difficult to fix it at a wind-proof elevated position above the ground.

As shown in Fig. 2, the degree of linear polarisation (d) of light reflected from the vertical and horizontal sticky black surfaces of our new tabanid trap depends on the direction of view but it is always high (70% < d < 90%) near the Brewster angle ($\theta_{Brewster}$ = arc tan (m) = 56.3° from the normal vector of the plastic surface with a refractive index of m = 1.5). The direction of polarisation of surface-reflected light is horizontal, if the plane of reflection is vertical. Thus, the horizontal surface of the trap always reflects horizontally polarised light. If the plane of reflection is horizontal or tilted, the reflected light is vertically or obliquely polarised. The consequence of these reflection-polarisation characteristics is that a predominant percentage (>90%) of the horizontal trap surface is always detected as water by water-seeking polarotactic tabanid flies. Light with degrees of polarisation d > 20% and angles of polarisation 80 < α < 100° means water for polarotactic tabanids (Kriska et al., 2009). On the other hand, depending on the direction of view, the vertical trap surface reflects light with horizontal, oblique or vertical direction of polarisation with high degrees of polarisation near the Brewster angle (Fig. 2). Thus the vertical horseflypaper attracts only host-seeking female tabanids.

Fig. 3A–C show the reflection-polarisation characteristics of a sunlit horizontal shiny black surface (plastic sheet, from which our test surfaces used in Experiments 1–3 were composed) measured from three different directions of view relative to the sun, when the polarimeter was oriented perpendicular to the solar meridian (Fig. 3A), toward the anti-solar meridian (Fig. 3B) and toward the solar meridian (Fig. 3C). According to these polarisation patterns, the light reflected from sunlit horizontal shiny black surfaces is always horizontally polarised, independent of the viewing direction with respect to the sun. The degree of polarisation d of surface-reflected light is higher or lower, depending on the elevation of view, but it is always high enough to attract tabanids. Fig. 3D and E show the reflection-polarisation characteristics of a shady horizontal shiny black surface measured under a totally overcast sky from two different directions of view, when the polarimeter was oriented perpendicular to the solar meridian (Fig. 3D) and toward the anti-solar meridian (Fig. 3E). Under overcast sky conditions the illumination of this surface had approximately a rotational symmetry, and thus the reflection-polarisation patterns of the surface were independent of the viewing direction relative to the invisible sun, as can also be seen in Fig. 3. The horizontal shiny black surface reflected linearly polarised light with high degrees of polarisation (represented by dark grey and black shades in row 2 of Fig. 3), and with exacty or nearly horizontal direction of polarisation. The consequence of these polarising characteristics is that the whole surface is sensed as water by polarotactic tabanids. This is the phenomenon that explains why a horizontal shiny (sticky) black surface is so strongly attractive to tabanids.

4. Discussion

The aim was to determine the ideal parameters of a new polarisation tabanid trap applying a modified concept of the old flypaper. Based on the positive polarotaxis of female and male tabanid flies, a trap composed of horizontal and vertical sticky black surfaces reflecting linearly polarised light with high degrees of polarisation at the Brewster angle and thus attracting polarotactic tabanids was designed. Like the classic flypaper, the new tabanid trap captured the attracted tabanids on the adhesive covering its surface. Because the target insects of this new sticky trap are tabanid flies, we call it "horseflypaper" as an analogy of the classic name "flypaper". In three field experiments we determined the ideal brightness, height, orientation and size of this horseflypaper. Experiment 1 determined that the ideal horseflypaper is black, contrary to the classic flypaper being usually bright. On the basis of Experiment 2, the ideal black horseflypaper is either horizontal laid on the ground, or vertical at approximately 1 m above the ground, contrary to the classic flypaper, which always hangs vertically several metres above ground level. In Experiment 3 it was determined that the ideal size of the black (horizontal or vertical) horseflypaper was approximately $75 \times 75\ cm^2$, since this size ensures a maximum surface density of catches, contrary to the classic flypapers which are usually a narrow strip.

Hence, by changing the colour of an old vertically hanging flypaper from chamois, light yellow or white to black, its narrow strip shape to a $75 \times 75\ cm^2$ square, its height from several metres to approximately 1 m above ground, and then its surface orientation from vertical to horizontal laid on the ground, we obtained an effective tool, the so-called "horseflypaper" to catch polarotactic tabanid flies. Based on the results of Experiments 1–3 a prototype of this horseflypaper composed of a horizontal and a vertical sticky black surface in an L-shaped arrangement was designed (Figs. 1D and 2). According to the results gathered from Experiment 4, this prototype functioned well and captured tabanids effectively under field conditions.

The fact that black is the ideal colour for the horseflypaper can be explained by the positive polarotaxis in tabanid flies. Tabanids are attracted to linearly polarised light, and the higher the degree of polarisation, the stronger the attraction (Horváth et al., 2008, 2010b; Egri et al., 2012a). Due to the rule of Umow (1905), the darker a shiny surface in a given spectral range, the greater the degree of linear polarisation of surface-reflected light. Thus, shiny black surfaces reflect light with the highest degrees of polarisation. Consequently, such surfaces are the most attractive to polarotactic tabanids.

In Experiment 4, the horizontal surface of the L-shaped combined horseflypaper caught 10.2 times more tabanids than the vertical surface (Table 4). In Experiments 1–3 similar results were obtained (Tables 1–3): the horizontal black test surfaces trapped approximately 15–23 times more tabanids than the vertical ones. The reason for the phenomenon that horizontal sticky black surfaces on the ground can trap many more tabanids than vertical ones could be as follows: earlier, it was shown that tabanids possess two different polarotaxis governed by different motivations (Egri et al., 2012a): (i) female tabanids that look for host animals to suck blood are attracted to dark targets reflecting linearly polarised light with high degrees of polarisation, independent of the direction of polarisation; (ii) water-seeking male and female tabanids are attracted to horizontally polarised light, since for them that light means water, because they detect water remotely by means of the horizontal polarisation of water-reflected light. Thus, the vertical sticky black test surfaces in our experiments trapped only those host-seeking female tabanids that wanted to suck blood for the development of their eggs. This host-finding period of female tabanids occurs mainly at the beginning of the tabanid season. On the other hand, the horizontal sticky black test surfaces in our experiments trapped all male and female tabanids that wanted (i) to drink water, and/or (ii) to cool the body in water, and/or (iii) to mate near water, and/or (iv) to lay eggs into/near water (females only). Motivations (i) and (ii) are characteristics of the whole tabanid season, while motivations (iii) and (iv) are typical at the beginning to the middle and the middle to the end of the tabanid season, respectively. Due to these more or less permanent motivations, the horizontal test surfaces maintained a strong attraction for male and female tabanids throughout the entire tabanid season; thus they captured many more tabanids than the corresponding vertical test surfaces.

The reason for the fact that in Experiment 4 the horizontal surface of the L-shaped horseflypaper trapped only 10 times as many tabanids as its vertical surface, while in Experiments 1–3 the horizontal test surfaces caught 15–23 times more tabanids than the corresponding vertical test surfaces, is that in Experiment 4 the vertical component of the L-shaped horseflypaper stood on the ground, while the ideal height of a vertical sticky black tabanid-trapping surface is approximately 1 m above ground. This is understandable, since black vertical surfaces imitate dark host animals which attract female tabanids that want to suck blood. A black vertical surface is more visible (and thus more attractive) from a more remote distance to flying host-seeking female tabanids if its height is approximately 1 m above the ground, rather than being at ground level.

It was found that a horizontal shiny black surface was attractive to tabanids only if it was on the ground. This can be explained in that such a horizontally polarising surface is sensed as water by flying tabanids, and the water surface is usually at ground level. Tabanids seem to know this and thus a horizontally polarising surface that is elevated from the ground is not interpreted as water by tabanids. This is rather surprizing, since certain other aquatic insects are attracted to horizontally polarising surfaces, even if these reflectors are elevated a few metres from ground level. For instance, certain non-biting midges (chironomids) are also polarotactic (Lerner et al., 2008), and their females are attracted to horizontally polarised light reflected from test surfaces laid on car rooves (Horváth et al., 2011).

We experienced that the ideal size of both the vertical and horizontal surface components of the L-shaped combined horseflypaper is approximately $75 \times 75\ cm^2$. Smaller or larger test surfaces trapped less tabanids per unit of area (surface density in Table 3). As mentioned above, vertical dark surfaces mimick host animals for host-seeking female tabanids. A given tabanid species may prefer a vertical dark surface with a particular size, that corresponds with the average size of the preferred or most common host animals. This preferred/optimal size may be tabanid species-specific. In the habitat of our field experiments 1–4 and in the case of the tabanid species investigated (*T. tergestinus*, *T. bromius*, *T. bovinus*, *T. autumnalis*, *Atylotus fulvus*, *A. loewianus*, *A. rusticus*, *H. italica*) the vertical size $75 \times 75\ cm^2$ was the most attractive to tabanids. Perhaps this is the most typical average size of host animals (horses, cattle, sheeps, dogs, humans) in this biotope.

On the other hand, the horizontal surface of our horseflypaper imitates a water surface for polarotactic water-seeking tabanids with the horizontally polarised reflected light. Considering drinking or body cooling by bathing, male and female tabanids may not prefer a water body of any particular size: tabanids could drink or bathe in practically every water body. However, female tabanids may prefer an optimally sized water body as their egg-laying site: too small water bodies can dry out quickly, hindering the development of tabanid larvae, while in too large water bodies fish can be predators of tabanid larvae. According to Experiment 3 (Table 3), on average the optimal size of oviposition sites seems to be approximately $75 \times 75\ cm^2$ for the tabanids investigated in this study. This optimal size could, however, be species-specific.

We did not study the optimal shape (e.g. triangular, rectangular, oval or elongated) of the horseflypaper because, in our opinion, this may not be an important variable. We have deterimined that the vertical and horizontal surfaces of the horseflypaper imitate host animals and water bodies, respectively, to tabanids. Both objects, as luring targets, usually have a shape, the vertical and horizontal dimensions of which are nearly equal. Thus, apart from the extreme case of an elongated shape (e.g. a strip), the exact form of the tabanid-attracting target may be irrelevant. A vertical strip cannot mimic a typical host animal of tabanids (e.g. snakes are not typical tabanid hosts). Similarly, a horizontal strip does not imitate a characteristic egg-laying site of tabanids (e.g. a narrow flowing water trickle is not ideal/optimal for the development of tabanid larvae). Thus, the strip shape of the classic flypaper is not appropriate for an ideal/optimal horseflypaper.

The ideal trap surface of $75 \times 75\,cm^2$ also has the advantage that it can be easily handled manually when the trap is transported, set up, refreshed and maintaned in the field. The handling and maintenance of much larger trap surfaces would be rather difficult, while much smaller trap surfaces would be not effective (Table 3; Supplementary Fig. S5).

It has been well documented that tabanids are generally attracted to dark, especially black objects, rather than bright ones (Granger, 1970; Roberts, 1970; Thompson and Pechuman, 1970; Anderson, 1985). Jones (1922), for example, reported on the attraction of male tabanids (mainly *T. bromius*) to small dark pools of water. Roth and Lindquist (1948) observed that female *Chrysops discalis* were attracted to oviposit on sticky dark boards and stakes set in the water along the shore of a lake. Blickle (1955) created artificial dark pools of water at which he caught tabanids. Von Kniepert (1979) placed a black plastic sheet (1.5×3 m) on the ground and caught, by hand-netting, several unspecified tabanid flies which were attracted to the plastic in a response identical to that of tabanids toward small water pools. Taylor and Smith (1989) captured *Tabanus sackeni* both on black plastic sheets and in dark water puddles. Using unbaited black sticky boards, Moore et al. (1996) trapped male tabanids. Hall et al. (1998) captured both male and female tabanids (*T. tergestinus* and *T. bromius*) using unbaited and odour-baited sticky black plastic sheets ($30 \times 30\,cm^2$) placed horizontally on the ground in a sheep pasture. Hence, in the past several researchers used horizontal sticky dark surfaces to capture tabanids. These sticky black test surfaces are the precursors of our new polarisation tabanid trap, horseflypaper. However, the cited researchers did not explain the exact reason for the attractiveness of their shiny dark test surfaces to tabanids. In all the above-mentioned earlier experiments, water-seeking tabanids were attracted by the horizontal polarisation of reflected light, which polarotactic behaviour was discovered only recently (Horváth et al., 2008).

The effects of brightness and colour on the visual attraction of some tabanid species have been thoroughly studied (Tashiro and Schwardt, 1953; Bracken et al., 1962; Granger, 1970; Roberts, 1970; Browne and Bennett, 1980; Allan and Stoffolano, 1986; Allan et al., 1987, 1991; Moore et al., 1996; Sasaki, 2001). Depending on species, white, blue, red/brown or black was found to be the most attractive colour for host-seeking tabanids. Because the reflection-polarisation characteristics of the coloured test surfaces/traps used in these experiments have never been measured, the relative role of polarisation and colour remained unknown in the attraction of tabanids. In our field experiments 1–4 we used white, grey and black test surfaces in order to eliminate the possible influence of wavelength-dependency on the attraction of tabanids.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ijpara.2013.02.002.

References

Allan, S.A., Stoffolano, J.G., 1986. The effects of hue and intensity on visual attraction of adult *Tabanus nigrovittatus* (Diptera: Tabanidae). J. Med. Entomol. 23, 83–91.
Allan, S.A., Day, J.F., Edman, J.D., 1987. Visual ecology of biting flies. Ann. Rev. Entomol. 32, 297–316.
Allan, S.A., Stoffolano, J.G., Bennett, R.R., 1991. Spectral sensitivity of the horse fly *Tabanus nigrovittatus* (Diptera: Tabanidae). Can. J. Zool. 69, 369–374.
Anderson, J.F., 1985. The control of horse flies and deer flies (Diptera: Tabanidae). Myia 3, 547–598.
Beavis, I.C., 1988. Insects and Other Invertebrates in Classical Antiquity. Exeter University Press, Exeter, UK.
Blahó, M., Egri, Á., Barta, A., Antoni, G., Kriska, G., Horváth, G., 2012a. How can horseflies be captured by solar panels? A new concept of tabanid traps using light polarization and electricity produced by photovoltaics. Vet. Parasitol. 189, 353–365.
Blahó, M., Egri, Á., Báhidszki, L., Kriska, G., Hegedüs, R., Åkesson, S., Horváth, G., 2012b. Spottier targets are less attractive to tabanid flies: on the tabanid-repellency of spotty fur patterns. PLoS ONE 7, e41138. http://dx.doi.org/10.1371/journal.pone.0041138.
Blickle, R.L., 1955. Observations on the habits of Tabanidae. Ohio J. Sci. 55, 308–310.
Bracken, G.K., Hanec, W., Thorsteinson, A.J., 1962. The orientation behavior of horseflies and deerflies (Tabanidae: Diptera). II. The role of some visual factors in the attractiveness of decoy silhouettes. Can. J. Zool. 40, 685–695.
Browne, S.M., Bennett, G.F., 1980. Color and shape as mediators of host-seeking responses of simuliids and tabanids (Diptera) in the Tantramar marshes, New Brunswick. Can. J. Med. Entomol. 17, 58–62.
Catts, E.P., 1970. A canopy trap for collecting Tabanidae. Mosquito News 30, 472–474.
Chadee, D.D., Ritchie, S.A., 2010. Oviposition behaviour and parity rates of *Aedes aegypti* collected in sticky traps in Trinidad. Acta Trop. 116, 212–216.
Coli, W.M., Green, T.A., Hosmer, T.A., Prokopy, R.J., 1985. Use of visual traps for monitoring insect pests in the Massachusetts apple IPM program. Agric. Ecosys. Environ. 14, 251–265.
Cross, J.V., Hesketh, H., Jay, C.N., Hall, D.R., Innocenzi, P.J., Farman, D.I., Burgess, C.M., 2006. Exploiting the aggregation pheromone of strawberry blossom weevil *Anthonomus rubi* Herbst (Coleoptera: Curculionidae): Part 1. Development of lure and trap. Crop Prot. 25, 144–154.
Egri, Á., Blahó, M., Sándor, A., Kriska, G., Gyurkovszky, M., Farkas, R., Horváth, G., 2012a. New kind of polarotaxis governed by degree of polarization: attraction of tabanid flies to differently polarizing host animals and water surfaces. Naturwissenschaften 99, 407–416.
Egri, Á., Blahó, M., Kriska, G., Farkas, R., Gyurkovszky, M., Åkesson, S., Horváth, G., 2012b. Polarotactic tabanids find striped patterns with brightness and/or polarization modulation least attractive: an advantage of zebra stripes. J. Exp. Biol. 215, 736–745.
Faiman, R., Kirstein, O., Moncaz, A., Guetta, H., Warburg, A., 2011. Studies on the flight patterns of foraging sand flies. Acta Trop. 120, 110–114.
Foil, L.D., 1989. Tabanids as vectors of disease agents. Parasitol. Today 5, 88–96.
Granger, C.A., 1970. Trap design and color as factors in trapping the salt marsh greenhead fly. J. Econ. Entomol. 63, 1670–1673.
Gressitt, J.C.L., Gressitt, M.K., 1962. An improved Malaise trap. Pac. Insects 4, 87–90.
Hall, M.J.R., Farkas, R., Chainey, J.E., 1998. Use of odour-baited sticky boards to trap tabanid flies and investigate repellents. Med. Vet. Entomol. 12, 241–245.
Harris, J.A., Hillerton, J.E., Morant, S.V., 1987. Effect on milk production of controlling muscoid flies, and reducing fly-avoidance behaviour by the use of Fenvalerate ear tags during the dry period. J. Dairy Res. 54, 165–171.
Hayakawa, H., 1980. Biological studies on *Tabanus iyoensis* group of Japan, with special reference to their blood-sucking habits (Diptera, Tabanidae). Bull. Tohoku Nat. Agric. Exp. Stat. 62, 131–321.
Horváth, G., Varjú, D., 1997. Polarization pattern of freshwater habitats recorded by video polarimetry in red, green and blue spectral ranges and its relevance for water detection by aquatic insects. J. Exp. Biol. 200, 1155–1163.
Horváth, G., Varjú, D., 2004. Polarized Light in Animal Vision – Polarization Patterns in Nature. Springer-Verlag, Heidelberg – Berlin – New York.

Horváth, G., Majer, J., Horváth, L., Szivák, I., Kriska, G., 2008. Ventral polarization vision in tabanids: horseflies and deerflies (Diptera: Tabanidae) are attracted to horizontally polarized light. Naturwissenschaften 95, 1093–1100.

Horváth, G., Blahó, M., Egri, Á., Kriska, G., Seres, I., Robertson, B., 2010a. Reducing the maladaptive attractiveness of solar panels to polarotactic insects. Cons. Biol. 24, 1644–1653.

Horváth, G., Blahó, M., Kriska, G., Hegedüs, R., Gerics, B., Farkas, R., Åkesson, S., 2010b. An unexpected advantage of whiteness in horses: the most horsefly-proof horse has a depolarizing white coat. Proc. R. Soc. B 277, 1643–1650.

Horváth, G., Móra, A., Bernáth, B., Kriska, G., 2011. Polarotaxis in non-biting midges: female chironomids are attracted to horizontally polarized light. Physiol. Behav. 104, 1010–1015.

Hribar, L.J., LePrince, D.J., Foil, L.D., 1991. Design for a canopy trap for collecting horse flies (Diptera: Tabanidae). J. Am. Mosq. Control Assoc. 7, 657–659.

Hribar, L.J., LePrince, D.J., Foil, L.D., 1992. Ammonia as an attractant for adult *Hybomitra lasiophthalma* (Diptera: Tabanidae). J. Med. Entomol. 29, 346–348.

Hunter, D.M., Moorhouse, D.W., 1976. The effects of *Austrosimulium pestilens* on the milk production of dairy cattle. Aust. Vet. J. 52, 97–99.

Jactel, H., Menassieu, P., Vétillard, F., Barthélémy, B., Piou, D., Frérot, B., Rousselet, J., Goussard, F., Branco, M., Battisti, A., 2006. Population monitoring of the pine processionary moth (Lepidoptera: Thaumetopoeidae) with pheromone-baited traps. Forest Ecol. Manag. 235, 96–106.

Jones, H., 1922. Some notes on the habits of male Tabanidae. The Entomol. 55, 40–42.

Kamarudin, N., Arshad, O., 2006. Potentials of using the pheromone trap for monitoring and controlling the bagworm, *Metisa plana* Wlk (Lepidoptera: Psychidae) on young oil palm in a smallholder plantation. J. Asia-Pacific Entomol. 9, 281–285.

von Kniepert, F.W., 1979. Eine leistungsfähige Methode zum Fang mannlicher Bremsen (Diptera, Tabanidae). Z. für Angew. Entomol. 88, 88–90.

Kriska, G., Bernáth, B., Farkas, R., Horváth, G., 2009. Degrees of polarization of reflected light eliciting polarotaxis in dragonflies (Odonata), mayflies (Ephemeroptera) and tabanid flies (Tabanidae). J. Insect Physiol. 55, 1167–1173.

Lehane, M.J., 2005. The Biology of Blood-Sucking in Insects, 2nd ed. Cambridge University Press, Cambridge, UK.

Lerner, A., Meltser, N., Sapir, N., Erlick, C., Shashar, N., Broza, M., 2008. Reflected polarization guides chironomid females to oviposition sites. J. Exp. Biol. 211, 3536–3543.

Luger, S.W., 1990. Lyme disease transmitted by a biting fly. New Engl. J. Med. 322, 1752–1759.

Malaise, R., 1937. A new insect-trap. Ent. Tidskr. Stockholm 58, 148–160.

Mihok, S., 2002. The development of a multipurpose trap (the Nzi) for tsetse and other biting flies. Bull. Entomol. Res. 92, 385–403.

Moore, T.R., Slosser, J.E., Cocke, J., Newton, W.H., 1996. Effect of trap design and color in evaluating activity of *Tabanus abactor* Philip in Texas rolling plains habitat. Southwestern Entomol. 21, 1–11.

Moreau, T.L., Isman, M.B., 2012. Combining reduced-risk products, trap crops and yellow sticky traps for greenhouse whitefly (*Trialeurodes vaporariorum*) management on sweet peppers (*Capsicum annum*). Crop Prot. 34, 42–46.

Roberts, R.H., 1970. Color of malaise trap and collection of Tabanidae. Mosquito News 29, 236–238.

Roberts, R.H., 1977. Attractancy of two black decoys and CO_2 to tabanids (Diptera: Tabanidae). Mosquito News 37, 169–172.

Roth, A.R., Lindquist, A.W., 1948. Ecological notes on the deer fly at Summer Lake. Oregon. J. Econ. Entomol. 41, 473–476.

Sasaki, H., 2001. Comparison of capturing tabanid flies (Diptera: Tabanidae) by five different color traps in the fields. Appl. Entomol. Zool. 36, 515–519.

Stejskal, V., 1995. The influence of food and shelter on the efficacy of a commercial sticky trap in *Tribolium castaneum* (Coleoptera: Tenebrionidae). J. Stored Prod. Res. 31, 229–233.

Taylor, P.D., Smith, S.M., 1989. Activities and physiological states of male and female *Tabanus sackeni*. Med. Vet. Entomol. 3, 203–212.

Tashiro, H., Schwardt, H.H., 1953. Biological studies of horseflies in New York. J. Econ. Entomol. 46, 813–822.

Thompson, P.H., Pechuman, L.L., 1970. Sampling populations of *Tabanus quinquetvittaus* about horses in New Jersey, with notes on the identity and ecology. J. Econ. Entomol. 63, 151–155.

Thorsteinson, A.J., Bracken, G.K., Hanec, W., 1965. The orientation behaviour of horseflies and deerflies (Tabanidae: Diptera). III. The use of traps in the study of orientation of tabanids in the field. Entomol. Exp. Appl. 8, 189–192.

Thorsteinson, A.J., Bracken, G.K., Tostawaryk, W., 1966. The orientation behaviour of horseflies and deerflies (Tabanidae: Diptera). VI. The influence of the number of reflecting surfaces on attractiveness to tabanids of glossy black polyhedra. Can. J. Zool. 44, 275–279.

Umow, N., 1905. Chromatische Depolarisation durch Lichtzerstreuung. Physik. Z. 6, 674–676.

Wall, W.J., Doane, O.W., 1980. Large scale use of box traps to study and control saltmarsh greenhead flies (Diptera: Tabanidae) on Cape Cod. Massachusetts. Environ. Entomol. 9, 371–375.

Wilson, B.H., Tugwell, N.P., Burns, E.C., 1966. Attraction of tabanids to traps baited with dry-ice under field conditions in Louisiana. J. Med. Entomol. 3, 148–149.