

An unexpected advantage of whiteness in horses: the most horsefly-proof horse has a depolarizing white coat

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White horses frequently suffer from malignant skin cancer and visual deficiencies owing to their high sensitivity to the ultraviolet solar radiation. Furthermore, in the wild, white horses suffer a larger predation risk than dark individuals because they can more easily be detected. In spite of their greater vulnerability, white horses have been highly appreciated for centuries owing to their natural rarity. Here, we show that blood-sucking tabanid flies, known to transmit disease agents to mammals, are less attracted to white than dark horses. We also demonstrate that tabanids use reflected polarized light from the coat as a signal to find a host. The attraction of tabanids to mainly black and brown fur coats is explained by positive polarotaxis. As the host's colour determines its attractiveness to tabanids, this parameter has a strong influence on the parasite load of the host. Although we have studied only the tabanid–horse interaction, our results can probably be extrapolated to other host animals of polarotactic tabanids, as the reflection–polarization characteristics of the host's body surface are physically the same, and thus not species-dependent.

Keywords: horses; tabanid flies; polarization vision; visual ecology; polarotaxis; host choice

1. INTRODUCTION

In nature, light grey, or albino (termed ‘white’ further on in this work) ungulates (e.g. horses) are rare because of their great vulnerability. They have a higher sensitivity to solar radiation often leading to malignant skin cancer and deficiency of the visual system (Pielberg *et al.* 2008). A white-coated animal is easily detected by predators, thus individuals with white coats have been selected out from wild populations during evolution. On the other hand, humans have bred a blood-line of ‘white’ horses just because of their rarity in the wild. To humans, the white horse became an icon for dignity, a status symbol demonstrating wealth (Tresidder 2005).

In this work, we show that white horses are less attractive to blood-sucking tabanid flies compared with dark horses. Our hypothesis is that this phenomenon can partly be explained by the polarization vision and positive polarotaxis in tabanids discovered recently (Horváth *et al.* 2008): tabanids are strongly attracted to all natural or artificial sources of horizontally polarized light. As horses and other mammals suffer considerably from tabanids, the tabanid-proof feature of host animals is advantageous in two respects: on the one hand, these blood-sucking flies are vectors of serious pathogens

(Foil 1989), and on the other hand, owing to their annoyance, horses and cattle cannot graze properly, thus suffering in economic parameters like body weight and milk production (Lehane 2005). In the long run, disturbed foraging and reduced food intake are expected to lead to negative effects on individual fitness in wild populations.

We performed field observations and choice experiments, in which the attraction of tabanids to living horses, test surfaces and horse models with different reflection–polarization characteristics was studied. To compare the polarizing characteristics of our horse models and test surfaces with those of typical host animals of tabanids, we measured the reflection–polarization patterns of living horses and cattle by imaging polarimetry. Our results show that the greater attraction of tabanids to darker hosts can be explained by the polarizing properties of the darker coat, rather than by the darker colour or higher temperature.

2. MATERIAL AND METHODS

(a) *Observation of tabanid–horse interaction*

We observed the reactions of a bay (termed ‘brown’ further on in this work) and a white horse to tabanid attacks on a sunny warm day (22 June 2008) on a field at Szokolya (47°52' N, 19°00' E), Hungary. We took 70 photographs

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Table 1. Habitation (+, occurrence; –, disappearance) of the white and the brown horses observed at Szokolya on 22 June 2008 versus time (=local summer time = UTC + 2 h), and the total time period t (minutes) spent by them in the shady forest and the sunny field.

time	shady forest		sunny field	
	white	brown	white	brown
11.00	–	–	+	+
11.15	–	+	+	–
11.25	+	+	–	–
11.30	–	–	+	+
11.40	–	+	+	–
11.43	–	–	+	+
11.46	–	+	+	–
11.49	–	–	+	+
11.58	–	–	+	+
11.59	–	+	+	–
12.02	–	+	+	–
12.03	–	+	+	–
12.04	+	+	–	–
12.23	–	+	+	–
12.30	+	+	–	–
13.00	+	+	–	–
t (min)	54	82	66	38

with 10 megapixel resolution of both horses each, and in the laboratory we counted the tabanids in these two sets of pictures. We measured the time periods spent by both horses in the sunny field and the shady forest bordering the field (table 1).

(i) Experiment 1

Experiment 1 was performed under sunny and warm weather conditions on 23–24 and 25–26 June 2008 on two horse farms at Szokolya (47°52' N, 19°00' E) and Göd (47°43' N, 19°09' E), respectively, between 09.30 and 17.30 h (universal time code (UTC) + 2 h). On the first day, a dry matte brown cloth (150 × 150 cm) was arranged on top of a wooden board on the ground. About one half (140 × 70 cm) of this cloth was covered by a transparent, colourless, 3 mm thick plastic sheet to make it appear shiny. The position of the plastic sheet was changed hourly: the plastic covered either the left, or the right half of the brown cloth. Furthermore, the brown cloth and the plastic sheet were moved every second hour from a shady place to a sunny one in the immediate vicinity of the observation point. The temperature T of the test surfaces was measured with a digital contact thermometer. T of both brown test surfaces was always the same (within an accuracy of $\pm 0.25^\circ\text{C}$). We counted the number of tabanids and their landings on both test surfaces. On the second day, the experiment was slightly altered: instead of the brown cloth, we used a matte white cloth.

(ii) Experiment 2

Experiment 2 was initially performed on 3 August 2008 from 09.00 to 19.00 h (UTC + 2 h) in a cemetery next to a riding school in Kiskunhalas (46°43' N, 19°5' E), Hungary. The experimental set-up was similar to the one used in the first experiment, but now the horizontal plastic sheet was covered by a colourless and odourless glue (BabolnaBio mouse trap) which trapped all insects that landed on the shiny test surface. Furthermore, the test surfaces were kept in the shadow. We

counted the tabanid landings on the matte dry brown surface, and counted the tabanids trapped by the sticky shiny brown surface. Upon being trapped by the glue, each tabanid was immediately removed from the test surface. This experiment was repeated on 4 August 2008 at the same site and just slightly altered: instead of the brown cloth, we used a matte white cloth. The temperature of all test surfaces used was the same, because they were all located in the shade.

The first part of this experiment, using matte dry brown and shiny sticky brown test surfaces, was replicated 10 times between 16 and 25 August 2009 at the same site from 12.00 to 13.00 h (UTC + 2 h) every day. Each tabanid trapped by the glue was immediately removed by the observer. However, the removal caused damage to the insects' bodies, such that taxonomical identification was impossible for those individuals. The insects could, however, clearly be identified as tabanid flies (Diptera: Tabanidae). The second part of this experiment, using matte brown and matte white test surfaces, was also replicated 10 times every day at the same site between 16 and 25 August 2009 from 13.00 to 14.00 h (UTC + 2 h).

(iii) Experiment 3

Experiment 3 was performed at the horse farm at Göd between 11 July and 7 September 2008. Five salad-oil-filled trays with different colour (white, light grey, medium grey, dark grey and black) were laid on the ground, and their relative order was changed randomly every day. The trays were covered during the night and when it was raining. The tabanids trapped by these trays were collected, stored in alcohol and later identified to species.

(iv) Experiment 4

Experiment 4 was carried out continuously between 17 July and 13 September 2009 at a horse farm at Szokolya (47°52' N, 19°00' E). One brown, one black and one white horse model (each with the same shape and dimensions; length 160 cm, height 110 cm, width 60 cm) was placed in a normal standing posture along a straight line on the grassy ground (figure 4) and 5 m apart from each other. The surfaces of the models were covered by a transparent, odourless and colourless insect monitoring glue (BabolnaBio mouse trap) every second day. Their relative positions were randomly changed every second day, but all three horse models were simultaneously either in the sun or in the shade. The tabanids trapped by the sticky surface of these horse models were counted and removed every second day (table 4). In a parallel experiment (lasting from 17 to 26 July, and from 11 to 16 August), we captured tabanid flies with a trap composed of a rectangular black plastic tray (50 × 50 cm) filled by a transparent salad oil. This capturing method enabled us to later determine the species of tabanids flying in the study site (table 4).

(b) Measurements of reflection–polarization characteristics

The reflection–polarization characteristics of test surfaces (figure 2), living horses and cattle (figure 3) as well as horse models (figure 4) were measured by imaging polarimetry in the red (650 ± 40 nm = wavelength of maximal sensitivity \pm half bandwidth of the charge coupled device detectors of the polarimeter), green (550 ± 40 nm) and blue (450 ± 40 nm) parts of the spectrum. In this work, we present only the polarization patterns measured in the blue spectral range. We

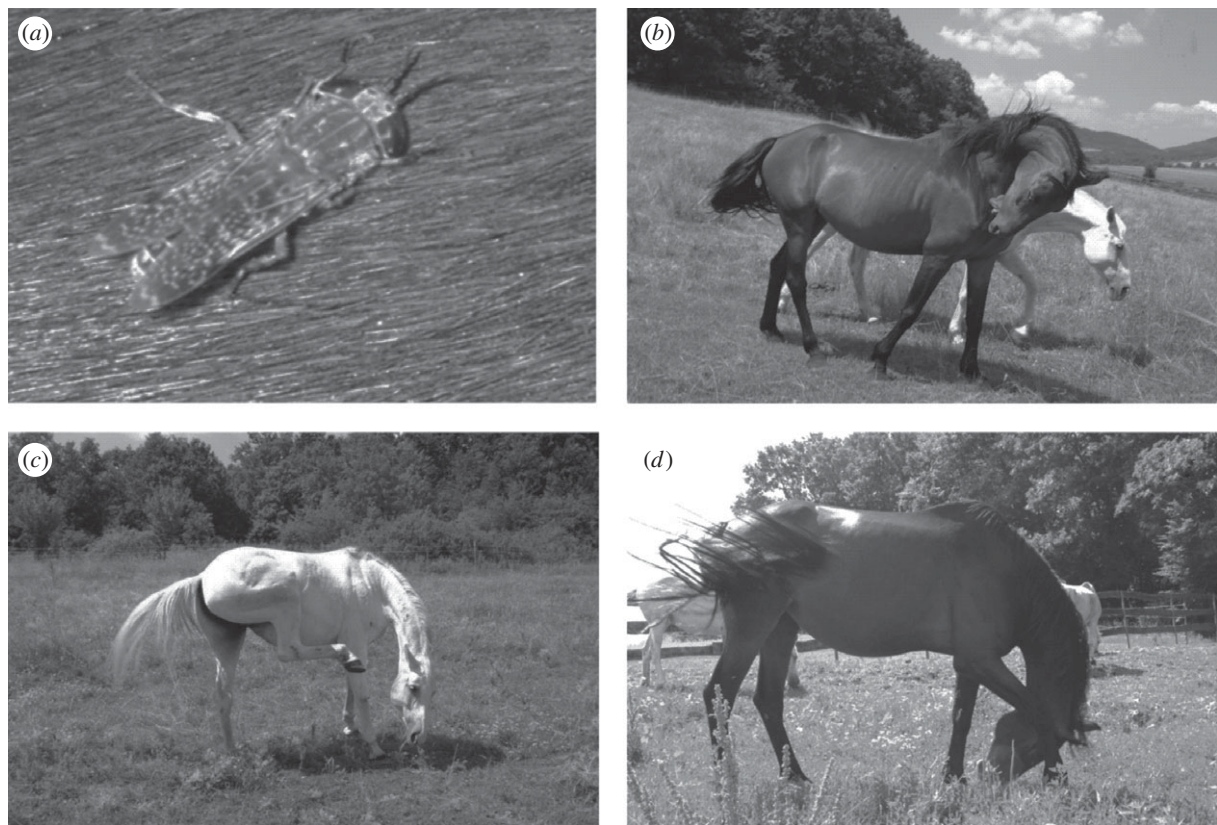


Figure 1. (a) A blood-sucking female tabanid on the coat of a brown horse. (b–d) Typical defensive reactions of brown and white horses to attacking tabanids: tail swishing (b–d), biting and licking the blood-sucking tabanids on the coat (b), and kicking with the legs (c,d).

recorded similar patterns in the red and green parts of the spectrum compared with in the blue spectral range. The method of imaging polarimetry has been described in detail by Horváth & Varjú (1997, 2004). All polarimetric measurements were performed under clear skies. An area of the water surface is sensed as water by polarotactic aquatic insects, tabanid flies, for example, if (i) the degree of linear polarization p of water-reflected light is higher than a threshold p^* and (ii) the deviation $\Delta\alpha = |90^\circ - \alpha|$ of the angle of polarization α from the horizontal ($\alpha = 90^\circ$) is smaller than a threshold $\Delta\alpha^*$ (Horváth & Varjú 2004). Both thresholds p^* and $\Delta\alpha^*$ are species-specific. As examples, in figure 4, we used $p^* = 10\%$ and $\Delta\alpha^* = 10^\circ$. Although these threshold values were arbitrarily selected, the use of other values did not qualitatively influence our results and conclusions.

(c) Taxonomic identifications

The taxonomic identification of the trapped tabanids conserved in ethyl alcohol was performed by one of the authors (R.F.).

(d) Statistics

Statistical analyses (analysis of variance (ANOVA) and binomial χ^2 -test) were carried out with the use of the computer program STATISTICA 6.0.

3. RESULTS

Both brown and white horses were attacked continuously by tabanids (figure 1a). Typical defensive reactions to tabanids, by which the horses tried to drive away these insects from their bodies, were tail swishing, kicking with the legs, rolling about on the ground, shuddering

of the skin, swinging the head, biting and licking the blood-sucking tabanids on the coat (figure 1b–d). Counting the numbers of tabanids in 70 picture pairs taken of a brown and a white horse, we found that there were on average 3.7 times (405/110) more tabanids near to or sitting on the brown horse compared with the white one, which is a statistically highly significant difference ($\chi^2 = 169$, d.f. = 1, $p < 0.0001$). The higher attractiveness of brown horses to tabanids relative to that of white horses was corroborated in our fourth experiment (see below).

Owing to the intense tabanid attacks, the horses shuttled between the sunny field and the shady surrounding forest (table 1): after a period spent grazing, the horses escaped from the aggressive tabanids into the shady forest refuge, where they suffered tabanid annoyance only rarely, thus they could rest and wait there quietly. After a certain period, the horses ventured out from the forest shade to graze again in the sunny field, from which they were soon again driven into the forest by tabanids. This shuttling was repeated by the horses periodically until midday (13.00 h), when the tabanid attacks became so intense that the horses could not graze any further in the field. It was always the brown horse that was first driven into the forest by the attacking tabanids (table 1). The brown horse spent 2.2 times (82/38 min) longer in the tabanid-free shady forest than in the sunny field, while the white horse stayed 1.2 times (66/54) longer in the sunny field, where it was able to continue to graze, than in the forest (table 1).

As it has recently been shown that numerous tabanid species are attracted to horizontally polarized light (Horváth *et al.* 2008), we hypothesized that the greater

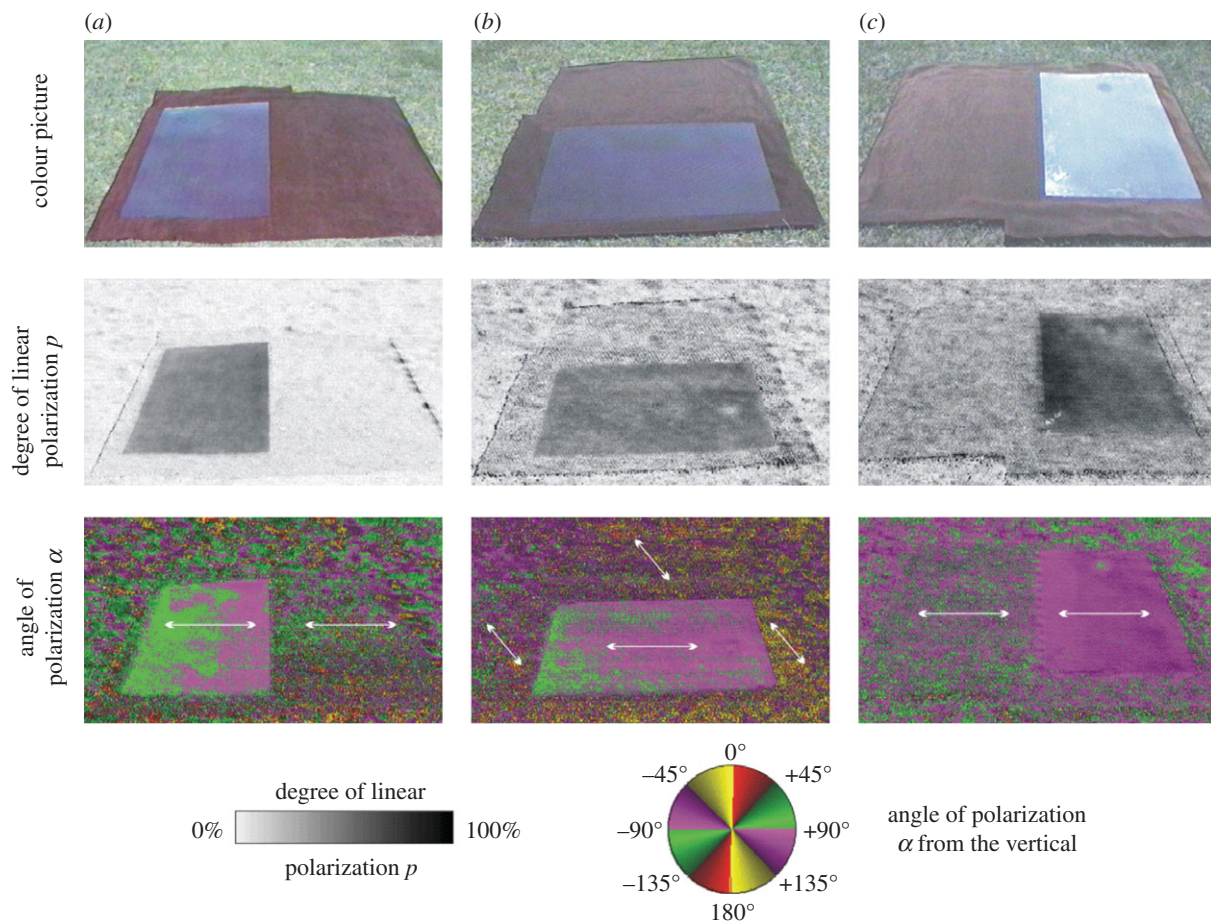


Figure 2. Reflection–polarization characteristics of the shiny brown and matte brown sunny test surfaces used in the first and second experiments measured by imaging polarimetry in the blue (450 nm) part of the spectrum from three different directions of view relative to the solar meridian. (a) Towards the antisolar meridian, (b) sun at right, normal to the solar meridian, and (c) towards the solar meridian. The elevation angle of the polarimeter’s optical axis was -35° from the horizontal. In the α -patterns, double-headed arrows show the local direction of polarization of reflected light. When the test surfaces were shady, their polarization patterns were quite similar with the only difference, that the direction of polarization of reflected light was always horizontal.

attractiveness of darker host animals to tabanids can partly be explained by the reflection–polarization characteristics of the host’s body surface. These characteristics depend strongly on the brightness and colour of the coat, as can be seen in figures 3 and 4. We tested this hypothesis in four field experiments.

In the first experiment, we realized that a dry matte brown cloth, imitating the coat of brown horses, was unattractive to tabanids (there was only one landing tabanid at both experimental sites at Szokolya and Göd). When the same matte brown cloth was turned into a shiny one (by being covered with a transparent, colourless plastic sheet), it attracted numerous tabanids (Szokolya: 44 tabanids with 174 landings, d.f. = 1, $p < 0.0001$, 44/1: $\chi^2 = 44.1$, 174/1: $\chi^2 = 171.0$; Göd: 47 tabanids with 157 landings, d.f. = 1, $p < 0.0001$, 47/1: $\chi^2 = 44.1$, 157/1: $\chi^2 = 154.0$). This statistically highly significant difference was independent of the illumination conditions (sunny or shady). The tabanids attracted to the cloth immediately landed on the plastic, or after 2–15 touch-downs. At both brown test surfaces, the tabanids displayed the same behaviour as in earlier choice experiments proving the positive polarotaxis in tabanids (Horváth *et al.* 2008). When we repeated the first experiment by using a matte dry brown and a matte dry white test surface, no tabanids were attracted at all.

In order to eliminate the pseudo-replication inevitably occurring in the first experiment (because the observed tabanids landing on the test surfaces could not have been marked), we performed the second experiment in which the majority of tabanids were trapped by a glue. The results of the second experiment corroborated those of the first experiment. In 2008, the brown cloth covered by a transparent, colourless, sticky plastic sheet trapped 21 tabanids, while the dry matte brown and matte white test surfaces attracted only 1 tabanid ($\chi^2 = 18.2$, d.f. = 1, $p < 0.0001$). In 2009, this experiment was replicated 10 times and according to table 2, the shiny sticky brown test surface trapped 189 tabanids, while the matte dry brown test surface attracted only four tabanids. Both years showed highly significant differences between the two test surfaces. In 2009, the second experiment was repeated 10 times with the use of a matte dry brown and a matte dry white test surface, and again no tabanids were attracted.

From the first and second experiments, we conclude that tabanids are not attracted to matte brown (weakly polarizing) and matte white (depolarizing) horizontal test surfaces, but they are attracted to shiny brown horizontal test surfaces, reflecting horizontally polarized light (figure 2). Consequently, the much larger attractiveness of brown horses to tabanids cannot be explained

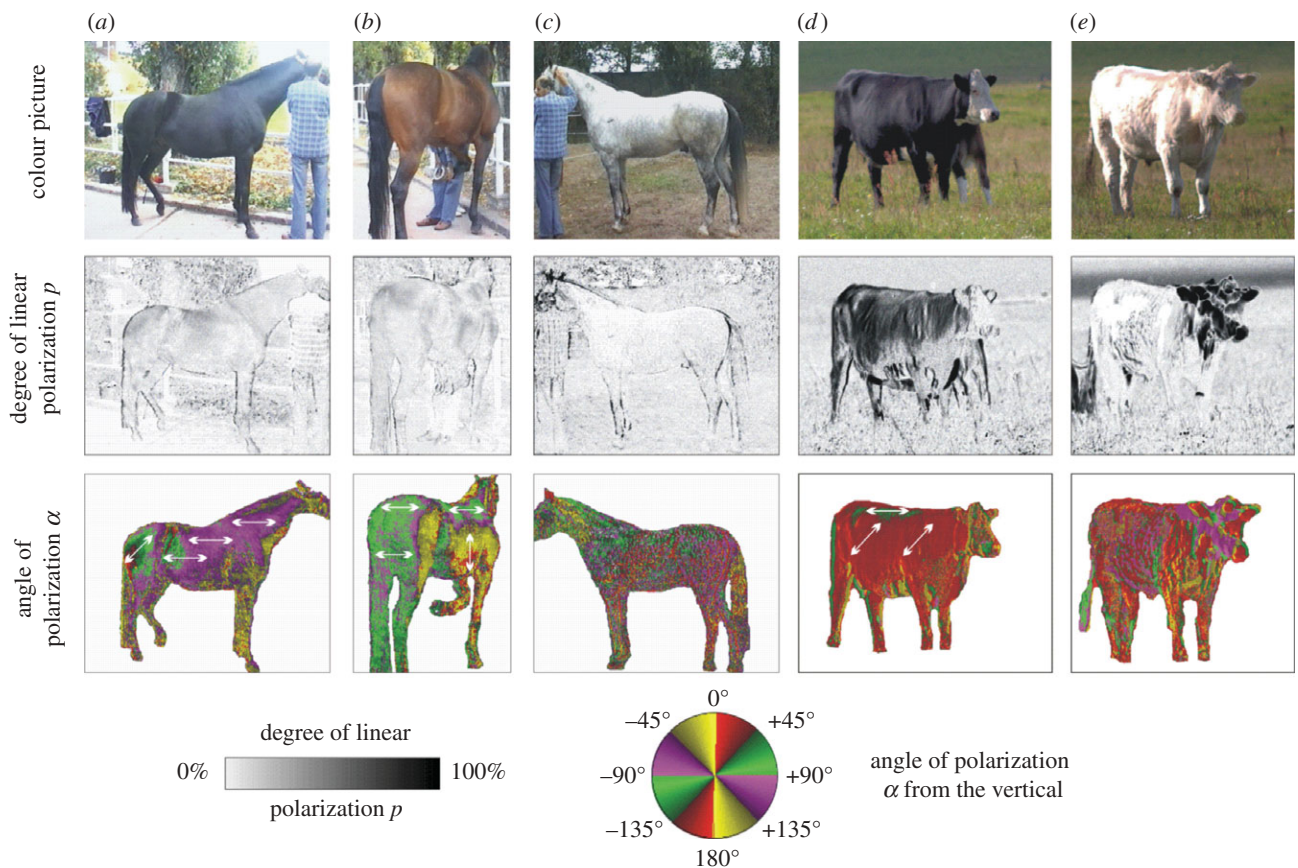


Figure 3. Reflection–polarization characteristics of (a) black, (b, bay) brown and (c, grey) white horses, and (d) black and (e) white cattle measured by imaging polarimetry in the blue (450 nm) part of the spectrum. In (d,e), the sun was shining from the top left corner. The optical axis of the polarimeter was horizontal. In the α -patterns, double-headed arrows show the local direction of polarization of light reflected from the horse/cattle coat, and the background of the horses is white for the sake of a better visualization. In (e), the bull moved its head during polarimetry, resulting in motion artefact, which is the reason for the artificially (unreal) high degrees of polarization p of its head. In reality, the head of the bull reflected unpolarized, or weakly polarized light as its whole body surface.

simply by the brightness and colour (white or brown) of the horse's coat. Independently of the viewing direction relative to the solar meridian, the shiny (dry or sticky) brown test surface always reflected horizontally polarized light with high degrees of polarization p , while the matte dry brown and matte dry white test surfaces reflected only weakly polarized light with direction of polarization depending on the direction of view relative to the sun (figure 2). Hence, not the brown colour, but the polarizing characteristics of the (matte or shiny) brown test surfaces determined their attractiveness/unattractiveness to tabanids in the first and second experiments.

This conclusion was further supported by the results of the third experiment (table 3), in which we found a positive correlation between the darkness of a colourless, shiny, horizontally polarizing test surface and its attractiveness to tabanids: the white, light grey and medium grey oil-filled trays trapped only 0.9–2.7% of the total number of tabanids, the dark grey tray captured 19.8 per cent, while the black tray trapped 74.8 per cent (table 3). This difference can be explained by the fact that the darker the trap surface, the higher the degree of polarization p of reflected light in all spectral ranges.

In the fourth experiment (figure 4 and table 4), the sticky brown and sticky black horse models trapped 15.2 (334/22) and 25.5 times (562/22) more tabanids

than the sticky white horse model, respectively. These differences are again statistically highly significant (statistics given in table 4). The distribution of trapped tabanids on the body surface of the sticky horse models was random; hence, neither body part was preferred by tabanids. According to figure 4, certain parts of the surface of both the brown and the black horse models reflected strongly and horizontally polarized light, while the whole surface of the white horse model reflected practically unpolarized light. The backside and the hindquarter of the brown and black sticky horse models reflected horizontally polarized light with high degrees of polarization (third row in figure 4), and thus these regions could be very attractive to flying polarotactic tabanids.

From our choice experiments and polarization measurements, we conclude that the higher the degree of horizontal polarization p of light reflected from a shady or sunny, brown or colourless (black or grey) surface, the larger its attractiveness to polarotactic tabanids. Based on this observation, we assume that the horizontally polarizing regions of the body surface of dark-coloured horses are more attractive to polarotactic tabanids than similar coat areas of light-coloured horses. According to figures 3 and 4, a darker coat reflects light with higher p : a black, brown and light grey/white coat

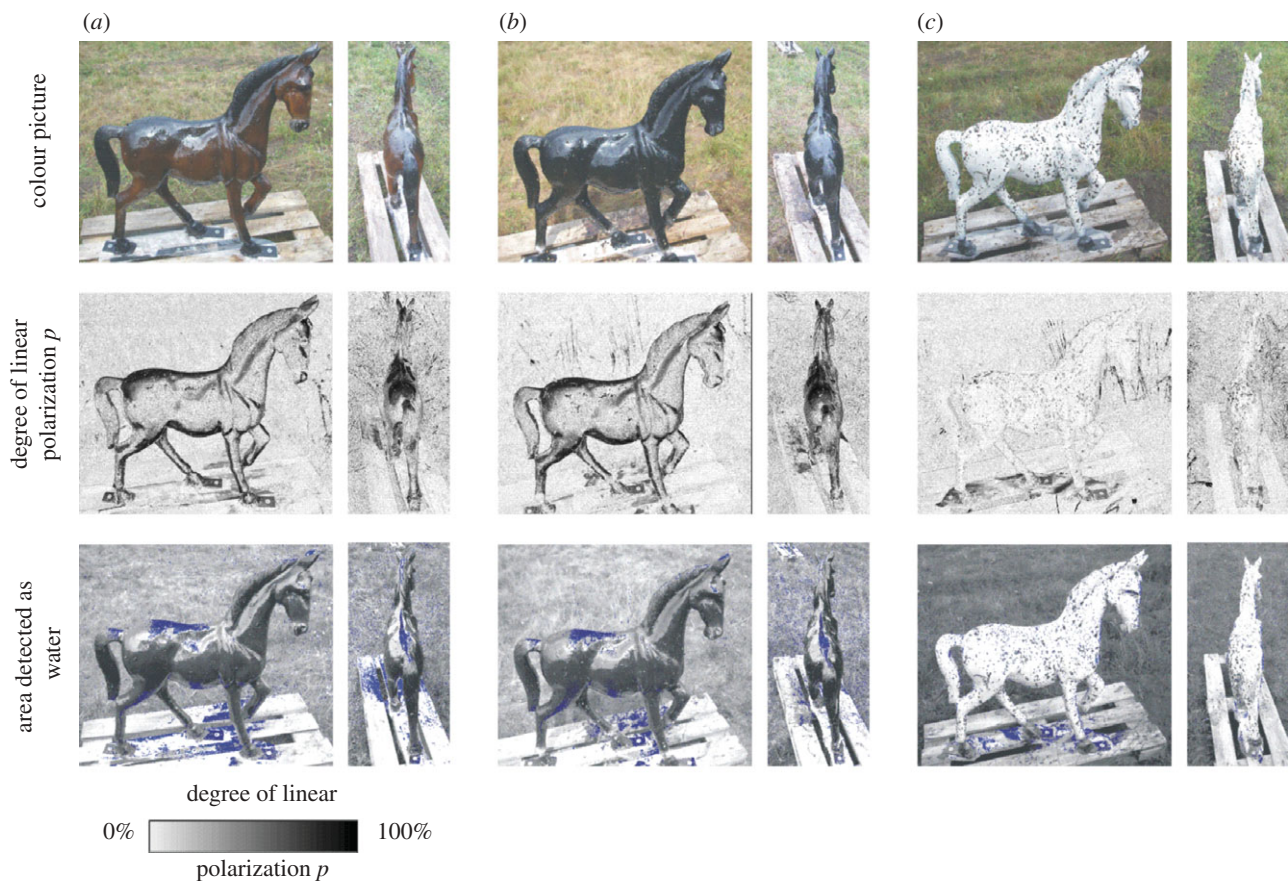


Figure 4. Colour pictures, patterns of the degree of linear polarization p and areas with apparently the same polarization characteristics as that of a water surface (i.e. areas detected as water by polarotactic insects, when the degree p and angle α of polarization of reflected light are in the following intervals: $10^\circ < p < 100^\circ$, $80^\circ < \alpha < 100^\circ$) measured by imaging polarimetry in the blue (450 nm) part of the spectrum from two different directions of view, for (a) the brown, (b) black and (c) white sticky horse models (covered by the carcasses of some trapped insects) used in the fourth experiment. The models were sunlit, and the optical axis of the polarimeter was -20° from the horizontal. In the third row, the areas detected as water are shown by the blue colour in the black-and-white pictures.

Table 2. Number n of tabanids landing on the matte dry brown test surface and trapped by the shiny sticky brown test surface in the second experiment in August 2009 (figure 2). (The difference between $n_{\text{shiny, sticky}} = 189$ and $n_{\text{matte, dry}} = 4$ is statistically highly significant (χ^2 -test: d.f. = 1, $\chi^2 = 177.3$, $p < 0.0001$; one-way ANOVA test: $SS_{\text{effect}} = 1711.3$, d.f. = 1, $MS_{\text{effect}} = 1711.3$; $SS_{\text{error}} = 443.3$, d.f. = 18, $MS_{\text{error}} = 24.6$; $F = 69.48$, $p < 0.0001$) and marked by an asterisk.)

date (2009)	matte dry brown	shiny sticky brown
16 August	1	25
17 August	0	22
18 August	1	13
19 August	0	32
20 August	1	15
21 August	0	16
22 August	0	19
23 August	1	25
24 August	0	12
25 August	0	10
sum	4	189*

reflects highly, moderately and weakly polarized or unpolarized light, respectively. Depending on the direction of view and illumination conditions, the neck, backside and hindquarters of horses and cattle in their standing

Table 3. Number n of tabanids (*Atylotus loewianus*, *Haematopota italica*, *Tabanus bovinus*, *T. maculicornis*, *T. tergstinus*) trapped by the salad-oil-filled white, light grey, medium grey, dark grey and black trays in the third experiment in Göd between 11 July and 7 September 2008. (The differences $n_{\text{black}} - n_{\text{dark grey}}$ ($\chi^2 = 35.44$, d.f. = 1, $p < 0.0001$) and $n_{\text{dark grey}} - n_{\text{medium grey}}$ ($\chi^2 = 14.44$, d.f. = 1, $p < 0.0001$) are statistically significant and marked by asterisks, while there are no statistically significant differences between the n -values of the white, light grey and medium grey trays: $n_{\text{white}} - n_{\text{light grey}}$ ($\chi^2 = 0.33$, d.f. = 1, $p = 0.56$), $n_{\text{light grey}} - n_{\text{medium grey}}$ ($\chi^2 = 0.2$, d.f. = 1, $p = 0.65$), $n_{\text{white}} - n_{\text{medium grey}}$ ($\chi^2 = 1$, d.f. = 1, $p = 0.32$).)

white	light grey	medium grey	dark grey	black
1 (0.9%)	2 (1.8%)	3 (2.7%)	22* (19.8%)	83** (74.8%)

posture usually reflect horizontally polarized light (encoded by bright violet and bright green colours in the α -patterns of figure 3), while other body parts reflect obliquely or vertically polarized light (encoded by red and yellow colours in the α -patterns of figure 3). These polarizing characteristics of the body surface are general and valid for all host animals of tabanids.

Table 4. Number n of tabanids (*Tabanus tergstinus*, *T. bromius*, *T. bovinus*, *T. autumnalis*, *Atylotus fulvus*, *A. loevianus*, *A. rusticus*, *Haematopota italica*) trapped by the sticky brown, black and white horse models in the fourth experiment. (The binomial differences $n_{\text{black}} - n_{\text{brown}}$ ($\chi^2 = 58$, d.f. = 1, $p < 0.0001$), $n_{\text{brown}} - n_{\text{white}}$ ($\chi^2 = 273.4$, d.f. = 1, $p < 0.0001$) and $n_{\text{black}} - n_{\text{white}}$ ($\chi^2 = 499.3$, d.f. = 1, $p < 0.0001$) are statistically highly significant, and marked by asterisks. The multinomial χ^2 -test also refers to statistically highly significant differences ($\chi^2 = 480.3$, d.f. = 2, $p < 0.0001$), like the one-way ANOVA test ($SS_{\text{effect}} = 5443.6$, d.f. = 2, $MS_{\text{effect}} = 2721.8$; $SS_{\text{error}} = 21132.4$, d.f. = 78, $MS_{\text{error}} = 270.9$; $F = 10.05$, $p < 0.0001$).

date (2009)	weather	sticky horse model		
		brown	black	white
17–18 July	sunny, warm	41	50	4
19–20 July	sunny, warm	23	33	2
21–22 July	sunny, warm	9	18	2
23–24 July	sunny, warm	35	59	2
25–26 July	sunny, warm	11	50	1
27–29 July	rainy, cool	0	0	0
30–31 July	sunny, warm	40	50	1
1–2 August	sunny, warm	64	78	2
3–4 August	sunny, warm	20	28	1
5–6 August	sunny, warm	10	13	1
7–10 August	overcast, cool	0	0	0
11–12 August	sunny, warm	15	58	0
13–14 August	sunny, warm	16	32	1
15–16 August	sunny, warm	21	40	0
17–18 August	sunny, warm	7	12	2
19–20 August	sunny, warm	9	19	2
21–22 August	rainy, cool	0	0	0
23–24 August	sunny, warm	1	5	0
25–26 August	sunny, warm	2	4	0
27–28 August	sunny, warm	2	6	0
29 August–	rainy, cool	0	0	0
1 September				
2–3 September	sunny, warm	2	4	0
4–5 September	sunny, warm	2	1	0
6–7 September	overcast, cool	0	0	0
8–9 September	sunny, warm	3	0	1
10–11 September	overcast, cool	0	0	0
12–13 September	sunny, warm	1	2	0
sum		334*	562**	22

4. DISCUSSION

Our results strongly support the hypothesis that the whiteness of the host's coat is an advantageous feature, because white hosts attract fewer parasitic tabanids than darker hosts. Many tabanid species are positively polarotactic, i.e. they are attracted to horizontally polarized light (Horváth *et al.* 2008), like aquatic insects in general (Schwind 1991; Wildermuth 1998; Horváth & Varjú 2004; Lerner *et al.* 2008). The positive polarotaxis in tabanids has adaptive significance in the following biological contexts: (i) it is used to guide female tabanids to potential egg-laying sites, from which the larvae can descend into water or moist mud; (ii) it is used to guide both male and female tabanids to water required for drinking and control of their body temperature; (iii) it can guide tabanids to locations where the different sexes can encounter each other; and (iv) it can provide female tabanids with an increased probability of finding hosts

(mainly social herbivores), also because the host animals regularly visit bodies of freshwater to drink and/or bath.

We propose that the polarotaxis of tabanids can also play an important role in their host choice: although differently coloured hosts should equally be appropriate as blood sources for female tabanids, these insects prefer darker (black, brown) hosts against brighter (light grey, white) ones, as shown here. This phenomenon can be explained partly by means of the polarizing characteristics of the body surface of the host and the polarotactic behaviour of tabanids. The coat of white host animals reflects light with lower degrees of polarization p than that of dark (brown or black) hosts. The physical reason for this is the following: the smooth surface of hair and skin reflects light specularly (i.e. the angle of incidence is equal to the angle of reflection) with highest p ($=100\%$) at the Brewster angle. The direction of polarization of this partially ($p < 100\%$) or totally ($p = 100\%$) polarized specular component is parallel to the reflecting surface. On the other hand, the light backscattered from the hair and skin tissues and refracted at their surfaces is weakly partially polarized ($p < 30\%$) with a direction of polarization perpendicular to the surface. Thus, this backscattered component reduces the p of the specular component, owing to their orthogonal directions of polarization. As for dark coats, the intensity of the backscattered component is much smaller than that of the specular component, the net p of coat-reflected light is high. For white coats, however, the net p of coat-reflected light is considerably reduced by the intense backscattered component.

Earlier, it has been shown that the motion, shape, brightness, colour, smell and heat of the host animals are important cues that govern host finding in tabanids (e.g. Thorsteinson 1958; Allan & Stoffolano 1986; Hall *et al.* 1998; Mihok 2002). The differential attraction of polarotactic tabanids as a result of colour-dependent polarization of coat-reflected light is likely to influence the diel behaviour of host animals, as was observed for the tabanid-attacked horses in our study, and for the evolution of honest signals used for mate choice (Hamilton & Zuk 1982).

According to our proposal, the tabanids investigated in our fourth experiment were partly attracted to the horse models (figure 4) by means of the horizontally polarized light reflected from certain parts of the models. Although from a remote distance, the horizontally polarizing parts of the body surface might have been the most attractive to polarotactic tabanids, their landing positions were distributed randomly on the whole surface. This demonstrates well that beyond the polarized light signal, other visual cues (brightness and colour of reflected light, shape of the host's body) also play an important role in the host choice of tabanid flies.

It is well known among horse-keepers that in shady refuges, in forests or in stables, for instance, horses suffer tabanid annoyance only rarely. Tabanid flies do not follow horses and other host animals in large numbers to such shady places more or less surrounded by vegetation or artificial walls. The reason for this is threefold: (i) tabanids need enough free, open space to fly; (ii) many tabanid species need a higher body temperature to start flying so quickly that they can successfully escape from the defensive reactions of a host animal

(e.g. tail swishing, biting, licking), by which the host tries to drive them away from its body. In shady refuges, the wing muscles of tabanids may not function rapidly enough for such an escape. Therefore, tabanids attack host animals usually under sunny conditions. For the same reason, tabanids usually do not fly and attack hosts on overcast days, and under rainy or too windy conditions. However, certain small-sized tabanids prefer periods prior to rain, because the lower air temperature and the higher air humidity are advantageous to these insects, whose body has a large surface/volume ratio, and thus they can easily become dehydrated under sunny, dry and windy conditions; or (iii) the forest vegetation, as a structured background, makes the visual recognition of host animals more difficult.

On the other hand, when looking for water by means of the horizontally polarized water-reflected light, tabanids can quickly fly through shady areas and touch the water surface to drink and/or bath, for example. This water-seeking behaviour of male and female tabanids is quite different from the blood-sucking behaviour of tabanid females. The former can happen under both shady and sunny conditions, while the latter is usually performed in sunshine. Nevertheless, water-seeking tabanids usually do not fly into dense forest vegetation. In our choice experiments, the horizontally polarizing test surfaces attracted both male and female tabanids, independent of the illumination conditions (sunny or shady), because these polarotactic insects sought water, rather than wanting to suck blood.

In temperate climates, potential tabanid hosts also include forest deer and elk, for instance, animals that prefer to consume vegetation in forest shade. Most of these forest-dwelling ungulates are dark-coloured to ensure an optimal camouflage in the darkness of vegetation. Our results obtained on horses cannot directly be extrapolated to these forest ungulates: although they have a dark coat, they might not be annoyed by tabanids, when feeding in the forest shade.

As tabanids are usually drab and darkish in colour, it is imaginable that in order to be less visible and to protect themselves from insectivorous birds, they prefer hosts that have more or less the same brightness, colour and polarization as the tabanid flies themselves. The chitinous body surface of tabanids itself also reflects partially linearly polarized light (G. Horváth 2008, unpublished data), the characteristics of which are similarly colour-dependent as those of the coat-reflected light. When white cattle egrets, for example, are sitting on the back of dark-coated cattle and pecking blood-sucking tabanids away from the cattle, tabanids blending in colour with that of their hosts fur might derive greater protection owing to camouflage. On the other hand, white egrets sitting on top of their hosts, according to our findings presented here, would be unattractive to tabanids and, thus, much less bothered by these flies than if the birds had brown or black plumages.

Although we studied only the tabanid–horse interaction, our results presented here can be generalized for other host animals of tabanids. The bases of this generalization are that positive polarotaxis seems to be general in tabanids (Horváth *et al.* 2008), and the polarizing characteristics of the body surface (figures 3 and 4) are physically the same for all host animals.

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