

RESEARCH ARTICLE

Polarotactic tabanids find striped patterns with brightness and/or polarization modulation least attractive: an advantage of zebra stripes

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SUMMARY

The characteristic striped appearance of zebras has provoked much speculation about its function and why the pattern has evolved, but experimental evidence is scarce. Here, we demonstrate that a zebra-striped horse model attracts far fewer horseflies (tabanids) than either homogeneous black, brown, grey or white equivalents. Such biting flies are prevalent across Africa and have considerable fitness impact on potential mammalian hosts. Besides brightness, one of the likely mechanisms underlying this protection is the polarization of reflected light from the host animal. We show that the attractiveness of striped patterns to tabanids is also reduced if only polarization modulations (parallel stripes with alternating orthogonal directions of polarization) occur in horizontal or vertical homogeneous grey surfaces. Tabanids have been shown to respond strongly to linearly polarized light, and we demonstrate here that the light and dark stripes of a zebra's coat reflect very different polarizations of light in a way that disrupts the attractiveness to tabanids. We show that the attractiveness to tabanids decreases with decreasing stripe width, and that stripes below a certain size are effective in not attracting tabanids. Further, we demonstrate that the stripe widths of zebra coats fall in a range where the striped pattern is most disruptive to tabanids. The striped coat patterns of several other large mammals may also function in reducing exposure to tabanids by similar mechanisms of differential brightness and polarization of reflected light. This work provides an experimentally supported explanation for the underlying mechanism leading to the selective advantage of a black-and-white striped coat pattern.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/215/5/736/DC1>

Key words: zebra, tabanid fly, horsefly, striped pattern, protection from parasites, visual ecology, reflection polarization, polarization vision.

INTRODUCTION

The most characteristic aspects of zebras are the bold black-and-white striped patterns on their body surface (Fig. 1). Embryological evidence (Prothero and Schoch, 2003) has shown that the background colour of zebras is black, and the white stripes and bellies (where the production of dark pigmentation is inhibited) appear only in a later embryonic developmental stage. The reason for the striped coat pattern in zebras has long been debated, and Wallace suggested that zebras evolved striped coats as camouflage against carnivores in tall grass (Wallace, 1867; Wallace, 1879). Darwin, however, who had closely studied the inheritance of colours and stripes in horses and zebras, criticized this hypothesis as an explanation (Darwin, 1871), as zebras do not occur in areas with dense vegetation but rather prefer open savannah habitats with short grass.

Since the 19th century, a number of alternative hypotheses (Waage, 1981; Ruxton, 2002; Lehane, 2005; Caro, 2009) have been proposed to explain the striped pattern of zebras, including predator defence, social interaction, indication of physical condition, thermoregulation, and protection from tsetse flies (a more detailed account is given in the Appendix). These and more explanations

have been thoroughly discussed and criticized by Ruxton (Ruxton, 2002) and Caro (Caro, 2009), who concluded that the majority of these hypotheses are experimentally unconfirmed, and thus the exact cause of stripes in zebras remains unknown. Nevertheless, the explanation of Waage (Waage, 1981) for the benefit of zebra stripes (i.e. protection from tsetse flies) has been the only hypothesis to be partially supported experimentally (Turner and Invest, 1973; Brady and Shereni, 1988; Gibson, 1992; Ruxton, 2002; Lehane, 2005; Caro, 2009).

Horseflies, or tabanids (Tabanidae), are vectors of several dangerous pathogens (Foil, 1989; Hall et al., 1998) and, if irritated by them, horses and cattle cannot graze, the consequence of which is the reduction of their body mass and milk production (Hunter and Moorhouse, 1976; Harris et al., 1987; Lehane, 2005). This suggests negative fitness consequences for animals that attract tabanid flies. Depending on the geographical distribution of different tabanid species in the vicinity of zebras in Africa (Uscher, 1972), these blood-sucking flies can also cause serious health problems for such equines (Leclercq, 1954; Kingdon, 1979; Moss, 1982; Leclercq and Maldes, 1987; Churcher, 1993; Leclercq, 2000; Tegegne, 2004). The tabanid larvae develop in water or mud, and both female

and male adults of many species are attracted to horizontally polarized light because they detect water by means of the horizontal polarization of water-reflected light (Horváth et al., 2008; Horváth et al., 2010). The consequences of this positive polarotaxis in tabanids are fivefold. (1) It attracts females to potential egg-laying sites, where larvae can descend into water. (2) It provides females with an increased probability of finding hosts, because social herbivores regularly visit fresh water. (3) It guides both males and females to water bodies, which they need for drinking and temperature control. (4) It drives both sexes of tabanids to locations where they can encounter each other. (5) Tabanids are less attracted to white compared with dark (e.g. brown or black) horses, and they also use reflected polarized light from the coat as one of the cues to find a host (Horváth et al., 2008; Horváth et al., 2010).

Since the zebra-striped pattern is intermediate to the white and black coats of horses, the attractiveness of zebras to tabanids might also be expected to be intermediate between those of white and black horses. We tested this hypothesis in six field experiments, in which we studied the attractiveness of striped and homogeneous dark and white horse models, of black-and-white striped test surfaces, or of homogeneous, colourless (grey) surfaces with polarization modulation (composed of parallel stripes of linear polarizers with alternating orthogonal directions of polarization) to polarotactic tabanids as a function of the stripe width. We measured the stripe width in different parts of zebra coats as well as the reflection-polarization characteristics of zebra coats and our test surfaces, using imaging polarimetry. Here, we present the results of these experiments and measurements, highlighting the evolutionary significance of striped coat patterns of hosts of polarotactic tabanid flies. We show that the attractiveness of striped patterns to tabanids decreases with decreasing stripe width and that the stripe widths of zebra coats fall in a range where the striped pattern is most disruptive to tabanids.

MATERIALS AND METHODS

Experiment 1

Experiment 1 was undertaken between 26 August and 12 September 2008 on a Hungarian horse farm at Szokolya (47°52'N, 19°00'E) to investigate the influence of the number of white orthogonal stripes on the attractiveness of horizontally polarizing black horizontal surfaces to tabanids. During the experiment, the weather was usually sunny and warm. Three plastic trays (50×50 cm) filled with salad oil (Vénusz vegetable oil, Bunge Növényolajipari Zrt., Budapest, Hungary) were placed on the ground (Fig. 3A; supplementary material Fig. S1). Salad oil was used because it traps tabanids efficiently and is transparent enough not to disturb the polarization characteristics of the test surfaces. This trapping method was tested successfully in our earlier field experiments (Horváth et al., 2008; Horváth et al., 2010; Kriska et al., 2009).

The first white-framed tray was painted homogeneously black without white orthogonal (perpendicular to each other) stripes ($N=0$, supplementary material Fig. S1A). The second and third white-framed painted black trays had two ($N=2$, supplementary material Fig. S1B) and six ($N=6$, supplementary material Fig. S1C) orthogonal painted white stripes (width=2 cm). The order of the trays was changed randomly every day. The trays were covered by wooden boards each night from sunset to sunrise and when it was raining. The tabanids trapped by the trays were collected, stored in alcohol and later identified (supplementary material Tables S1, S2). Although the whole area of all three trays was the same ($A=0.25\text{ m}^2$), the sum $A_{\text{black}}(N)$ of their black areas was slightly different owing to the different numbers (N) of white stripes. The larger the number N of

these stripes, the smaller the highly and horizontally polarizing black area $A_{\text{black}}(N)$, and thus the smaller the predicted attractiveness to polarotactic tabanids:

$$\begin{aligned} A_{\text{black}}(N=0) &= (50\text{ cm} - 2 \times 2\text{ cm})^2 = 0.2116\text{ m}^2, \\ A_{\text{black}}(N=2) &= 4 \times [(50\text{ cm} - 3 \times 2\text{ cm})/2]^2 = 0.1936\text{ m}^2, \\ A_{\text{black}}(N=6) &= 16 \times [(50\text{ cm} - 5 \times 2\text{ cm})/4]^2 = 0.1600\text{ m}^2. \end{aligned}$$

The motivation for making these area calculations is to compare correctly the numbers of trapped tabanid flies: the number m of tabanids captured by a given tray was divided by the black area $A_{\text{black}}(N)$, resulting in the surface density $n=m \times 1\text{ m}^2/A_{\text{black}}(N)$, giving the number of flies captured by 1 m² black tray surface. These densities are also given in supplementary material Table S1.

Experiment 2

Experiment 2 was performed at a Hungarian horse farm in Göd (47°43'N, 19°09'E) between 1 July and 5 September 2009 to study the dependence of the attractiveness of horizontal striped surfaces to tabanids on the stripe width. Five plastic trays filled with salad oil (Fig. 3A; supplementary material Fig. S2) were placed on the ground, and their order was changed randomly every 5 days. There were two small (35.5×35.5 cm) and three large (50×50 cm) trays. One of the small trays was painted black (supplementary material Fig. S2A) while the other was painted white (supplementary material Fig. S2E), both having a surface area of $A_{\text{small}}=0.1260\text{ m}^2$. The three large trays were painted so that they had 1–1 (supplementary material Fig. S2B), 3–3 (supplementary material Fig. S2C) and 6–6 (supplementary material Fig. S2D) black–white parallel stripes with the same total area $A_{\text{black}}=A_{\text{white}}=0.1250\text{ m}^2$. Hence, the total black or white area of the three striped large trays was practically the same as the area of the two small homogeneous trays: $A_{\text{black}}=A_{\text{white}}=0.1250\text{ m}^2 < A_{\text{small}}=0.1260\text{ m}^2$. The two homogeneous trays functioned as controls, with the same area as the total black or white areas of the striped trays. When considering the dependence of tabanids trapped by the striped trays on the stripe width, the catches of these homogeneous trays were not taken into account. The trays were covered by wooden boards every day from sunset to sunrise and when it was raining. The tabanids trapped by these trays were collected every 5 days (supplementary material Table S3), stored in alcohol and later identified (supplementary material Table S4).

Experiment 3

Experiment 3 was conducted between 17 August and 13 September 2009 at the same horse farm as experiment 1 and was designed to study the landing position of tabanids on horizontal striped patterns. In experiments 1 and 2, tabanids were trapped by salad oil and, after trapping, their carcasses could drift arbitrarily in the oil. Thus, it was unknown whether initially they landed on a black or a white part of the striped test surfaces. This problem was eliminated in experiment 3, where tabanids were captured by a glue, fixing their landing position. Three different horizontal black-and-white striped test surfaces (50×50 cm) composed of thin plastic boards were placed on the ground (Fig. 3A). Their surfaces were covered with transparent, odourless and colourless insect monitoring glue (BabolnaBio[®] mouse trap, Bábólna Bio Ltd, Bábólna, Hungary). Their order was changed randomly, when the trapped tabanids were counted and removed from the glue (supplementary material Table S5). The glue was refreshed twice a week. The 1st, 2nd and 3rd test surface had 1–1, 2–2 and 4–4 black–white parallel stripes with the same total area $A_{\text{black}}=A_{\text{white}}=0.1250\text{ m}^2$. After rain, when the sticky test surfaces became dry, the glue continued to trap insects.

Experiment 4

Experiment 4 was carried out between 17 July and 13 September 2009 at the same horse farm as experiment 1 and was designed to investigate the attractiveness to tabanids of three-dimensional horse-shaped targets with different colour patterns. A brown, a black, a white and a black-and-white zebra-striped horse model (Fig. 2A,B, Fig. 3A) composed of plastic, each with the same shape and dimensions (length=160 cm, height=110 cm, width=60 cm) were placed in a normal standing posture on the grassy ground, 5 m apart from each other along a straight line. The pattern of the zebra-striped horse model was copied from a real zebra skin, and the ratio of the black and white surface regions was approximately 1:1. Their surfaces were covered with transparent, odourless and colourless insect monitoring glue (BabolnaBio® mouse trap) twice a week, and their positions were then also randomly changed. Due to their positions, all four horse models were simultaneously either in the sun or in the shade. In sunny and warm weather, the tabanids trapped by the sticky surface of these horse models were counted and removed every 2 days (a total of 27 times). When the weather was rainy/overcast and cool, tabanids did not fly and thus the sticky horse models did not capture any tabanid flies.

Experiment 5

Experiment 5 was conducted between 16 July and 26 August 2010 at the same horse farm as experiment 1 to test the effect of both the width and the angle (direction) of stripes on vertical surfaces on the attractiveness to tabanids, because in experiments 1–3 only horizontal striped test surfaces were used. Six different vertical test surfaces (100×100 cm), composed of thin plastic board, were fixed to vertical metal rods stuck into the ground 2 m apart along a straight line. There was one chequered (Z1), one white (W), one grey (G) and three striped (Z2, Z5, Z13) test surfaces. The chequered surface had two white and two black equal squares in a diagonal arrangement. The three black-and-white striped surfaces were composed of four equal squares with the same stripe width but with four different stripe orientations: vertical, horizontal, +45 deg and –45 deg relative to the vertical. The 1st, 2nd and 3rd striped test surface had 13×4, 5×4 and 2×4 black stripes with a width (w) of 2.0, 6.0 and 12.5 cm, respectively, and the total area of their black and white stripes was the same. A given test surface had the same pattern on both sides. The greyness of the grey test surface was 50%, coinciding with the average greyness of the black-and-white striped test surfaces Z1, Z2, Z5, Z13 (Fig. 3A). The test surfaces were covered with transparent, odourless and colourless insect monitoring glue (BabolnaBio® mouse trap). Their order was changed randomly every week. When the trapped tabanids were counted and removed from the sticky test surfaces (supplementary material Table S6), the glue was refreshed. Between 16 July and 5 August, only the front side of the test surfaces (facing towards a meadow) was glued. Between 6 and 26 August, the test surfaces were turned over and both their sides (front and back) were glued. Then the tabanids trapped by the two sticky sides were counted separately (supplementary material Table S6).

Experiment 6

Experiment 6 was conducted between 25 June and 1 September 2011 at the same horse farm as experiment 1 to study how the direction of polarization influences the attractiveness to tabanids independently of the direction of striping. To test the role of polarization in the attractiveness of striped patterns to polarotactic tabanids, we used three different striped test surfaces (43×43 cm): Surface Z9+ was composed of nine linearly polarizing neutral grey

parallel stripes (P-W-44, Schneider, Bad-Kreuznach, Germany) with alternating orthogonal transmission directions (supplementary material Fig. S3C). Surface Z17+ was made of 17 linearly polarizing parallel stripes (P-W-44) with alternating orthogonal transmission directions (supplementary material Fig. S3B). Surface Z17_ was composed of 17 linearly polarizing parallel stripes (P-W-44) with parallel transmission directions (supplementary material Fig. S3A). The stripe width of test surfaces Z17+, Z9+ and Z17_ was (Fig. 3A) $w=43/17=2.5$, $43/9=4.8$ and 43 cm, respectively. Z17_ had a homogeneous (constant) direction of polarization and was considered as a single 'stripe'.

The substrate of the linearly polarizing stripes was a wooden board (43×43×2 cm) painted matt white. The polarizing stripes were fixed (with tiny nails) parallel to each other, contacting at their margins as tightly as possible on the white substrate. We used one pair of each surface type: the first surface was laid horizontally on the ground, and the second one was fixed at a height of 1 m above the ground between vertical metal rods stuck into the ground. The horizontal distance of the two test surfaces of the same type was 1 m. The three pairs of test surfaces were set along a straight line 5 m apart from each other. The test surfaces were covered by a transparent, odourless and colourless insect monitoring glue (BabolnaBio) every 3–4 days. We counted the tabanids trapped by these sticky test surfaces periodically, when all other insects captured were also removed and the order of the test surfaces was randomized.

The brightness and colour of the test surfaces were the same (greyness=25%), but the patterns of the degree and direction of polarization were different due to the different transmission directions of the polarizing stripes (supplementary material Fig. S3). Surfaces Z9+ (supplementary material Fig. S3C) and Z17+ (supplementary material Fig. S3B) presented striped patterns only in the state of polarization, while surface Z17_ displayed a homogeneous pattern in brightness, colour and polarization. At the contacting edges of the polarizing stripes, there was inevitably a weak brightness contrast. Such contrast lines occurred in all six test surfaces, because Z17_ functioning as a control surface with a homogeneous polarization pattern, was also composed of linearly polarizing stripes.

Measurements of reflection–polarization characteristics

To compare the reflection–polarization patterns of our test surfaces with those of a zebra coat, the polarizing characteristics of the test surfaces (Fig. 2A,B, supplementary material Figs S1–S3) were measured by imaging polarimetry 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. We also measured the polarization characteristics of a real-size zebra model covered by a coat of *Equus burchelli* (Fig. 2C–G) in the courtyard of the Hungarian Natural History Museum in Budapest. In this work, we present only the polarization patterns measured in the blue spectral range, to which tabanids are shown to be sensitive (Allan et al., 1991; Mihok, 2002; Lehane, 2005). Similar patterns were obtained in the red and green parts of the spectrum. The test surfaces composed of black-and-white stripes or linearly polarizing stripes used in our experiments were colourless, thus their reflection–polarization characteristics were practically independent of the wavelength of light. Consequently, the polarization patterns of our test surfaces measured in the blue spectral range were very similar to those in the UV. The method of imaging polarimetry has been described in detail elsewhere (Horváth and Varjú, 1997;

Horváth and Varjú, 2004). The polarimetric measurements were performed in sunshine, under clear skies. An area of a polarizing reflector is sensed as water by polarotactic tabanid flies (as well as by aquatic insects in general) if (i) the degree of linear polarization (d) of reflected light is higher than a threshold (d^*) and (ii) the deviation $\Delta\alpha=|90-\alpha|$ of the angle of polarization α from the horizontal ($\alpha=90$ deg) is smaller than a threshold $\Delta\alpha^*$ (Horváth and Varjú, 2004; Horváth et al., 2008). Both thresholds d^* and $\Delta\alpha^*$ depend on species (Kriska et al., 2009). As examples, in Fig. 2 and supplementary material Figs S1 and S2 we used $d^*=10\%$ and $\Delta\alpha^*=10$ deg. Although these threshold values are rather arbitrary, the use of other values did not qualitatively influence our results and conclusions.

The physical reason why dark areas polarize reflected light more efficiently is as follows. The light reflected from the surface of an object is parallelly polarized to the surface. On the other hand, the light coming from the subsurface regions is perpendicularly polarized to the surface. The net polarization of light returned by the object is determined by the polarization characteristics of these two components. If the first component dominates, the direction of polarization of returned light is parallel to the surface; otherwise it is perpendicular. Both components reduce the polarization of each other. The more dominant a component, the higher is the degree of linear polarization d of returned light. If the intensities of the two components are approximately equal, then $d=0\%$. In the case of dark surfaces, the first component dominates, thus d is high. For bright surfaces, the polarization of the first component is drastically reduced by that of the second component. This results in a low d . This is the so-called Umow effect (Umow, 1905).

Measurement of stripe width on zebra coats

In order to compare the stripe widths of the test surfaces used in experiments 1–6 with those of real zebras, we measured the stripe width on coats of *E. burchelli* (13 coats) and *E. grevyi* (5 coats) in the Hungarian Natural History Museum (Budapest), and *E. zebra* (1 coat) in the Swedish Natural History Museum (Stockholm). We selected relatively uniformly striped regions on the head, neck, abdomen-side, back-side, front leg and hind leg on the zebra coats (supplementary material Fig. S4), and measured the average and standard deviation of the width of white and black stripes by a digital slide-gauge. In experiments 2, 3, 5 and 6, the relative proportions of the white and black stripes and the linearly polarizing stripes of the test surfaces (supplementary material Fig. S2) were equal (50–50%), and the same was true for the zebra-striped horse model used in experiment 4 (Fig. 2A,B). This was important – otherwise the preference of the black or white stripes or the differently polarizing stripes by tabanids could also be explained by the inequality of the black and white or the differently polarizing regions of the test surfaces.

Identification of tabanids

Tabanids trapped by the trays filled with salad oil were preserved in ethyl alcohol and identified in the laboratory. When the trapped tabanids were removed from the insect monitoring sticky surfaces used in experiments 3–6, their bodies suffered such serious damage that their taxonomical identification was impossible. They were, however, unambiguously identified as tabanid flies (Diptera: Tabanidae). In a parallel experiment lasting from 17 to 26 July and from 11 to 16 August 2009, we captured tabanids with a trap composed of a rectangular black plastic tray (50×50 cm) filled with a transparent salad oil. This method of capture made it possible to determine the eight species of tabanids (*Tabanus tergustinus*, *T.*

bromius, *T. bovinus*, *T. autumnalis*, *Atylotus fulvus*, *A. loewianus*, *A. rusticus*, *Haematopota italica*) flying in the study site during experiments 3–6 (supplementary material Tables S2, S4).

Statistics

For statistical analyses (ANOVA and binomial χ^2 -test), we used Statistica 7.0 (StatSoft, Hungary Ltd, Budapest, Hungary).

RESULTS

In experiment 1, we found that the denser the white grid on white-framed black trays filled with salad oil, the smaller the number of trapped tabanids (supplementary material Tables S1, S2). The white-framed black tray without orthogonal white stripes (supplementary material Fig. S1A) captured a significantly higher number ($m=247$) of tabanids than the white-framed black trays with 2 (Fig. 3A; supplementary material Fig. S1B) and 6 (supplementary material Fig. S1C) orthogonal white stripes ($m=185$ and 33, respectively) (χ^2 test: $\chi^2=108.60$, d.f.=2, $P<<0.001$). This change in tabanid numbers cannot be explained simply by the reduction in black surface; the surface densities (n) of trapped tabanids were $n=1167.3$, 955.6 and 206.3 for the trays without ($N=0$) and with $N=2$ and 6 orthogonal white stripes, respectively (supplementary material Tables S1, S2). The white stripes reflected unpolarized light, while the black areas of these trays reflected highly and horizontally polarized light, which is very attractive to polarotactic tabanids (Row 4 in supplementary material Fig. S1). The main effect comes from the fact that the white stripes break up the uniform black surface. This experiment demonstrates that black surfaces reflecting horizontally polarized light are less attractive to tabanids if the number of depolarizing white stripes increases.

In experiment 2, the white and black trays filled with salad oil were, respectively, the least and the most attractive to tabanid flies, with 3 versus 145 trapped individuals (supplementary material Tables S3, S4). The smaller the number N of black/white stripes, the more tabanids were trapped; the trays with $N=12$, 6 and 2 stripes captured 24, 66 and 138 tabanids, respectively (χ^2 test: $\chi^2=88.62$, d.f.=4, $P<<0.001$; supplementary material Tables S3, S4).

In experiment 3, the horizontal sticky 2-striped test surface attracted most tabanids ($N=321$), the 4-striped surface was less attractive ($N=290$) and the 8-striped surface was the least attractive ($N=19$), resulting in significant differences in the number of trapped tabanids between the different groups (χ^2 test: $\chi^2=262.87$, d.f.=2, $P<<0.001$; supplementary material Table S5). The insect monitoring sticky surface fixed the landing position of insects attracted. Thus, we could observe that the highly polarizing shiny black stripes attracted 14/5=2.8 times (8-striped test surface), 225/65<3.5 times (4-striped test surface) and 265/56<4.7 times (2-striped test surface) more tabanids than the weakly polarizing shiny white stripes (supplementary material Table S5). Under all conditions, we found significantly higher numbers of tabanids trapped on the black stripes compared with the white stripes (χ^2 test: 2 stripes, $\chi^2=136.08$, d.f.=1, $P<0.001$; 4 stripes, $\chi^2=88.28$, d.f.=1, $P<0.001$; 8 stripes, $\chi^2=5.0$, d.f.=1, $P<0.025$).

In experiment 4, the black ($N=562$) and brown ($N=334$) horse models were the most attractive to tabanids, the white model ($N=22$) was much less attractive [see table 4 of Horváth et al. (Horváth et al., 2010)] and, interestingly enough, the black-and-white zebra-striped horse model ($N=8$) was the least attractive. There were significant differences between the numbers of tabanids attracted to these horse models. Notably, in spite of the small numbers of captured tabanids, the difference between the zebra-striped (Fig. 2A,B) and the white sticky horse models was significant

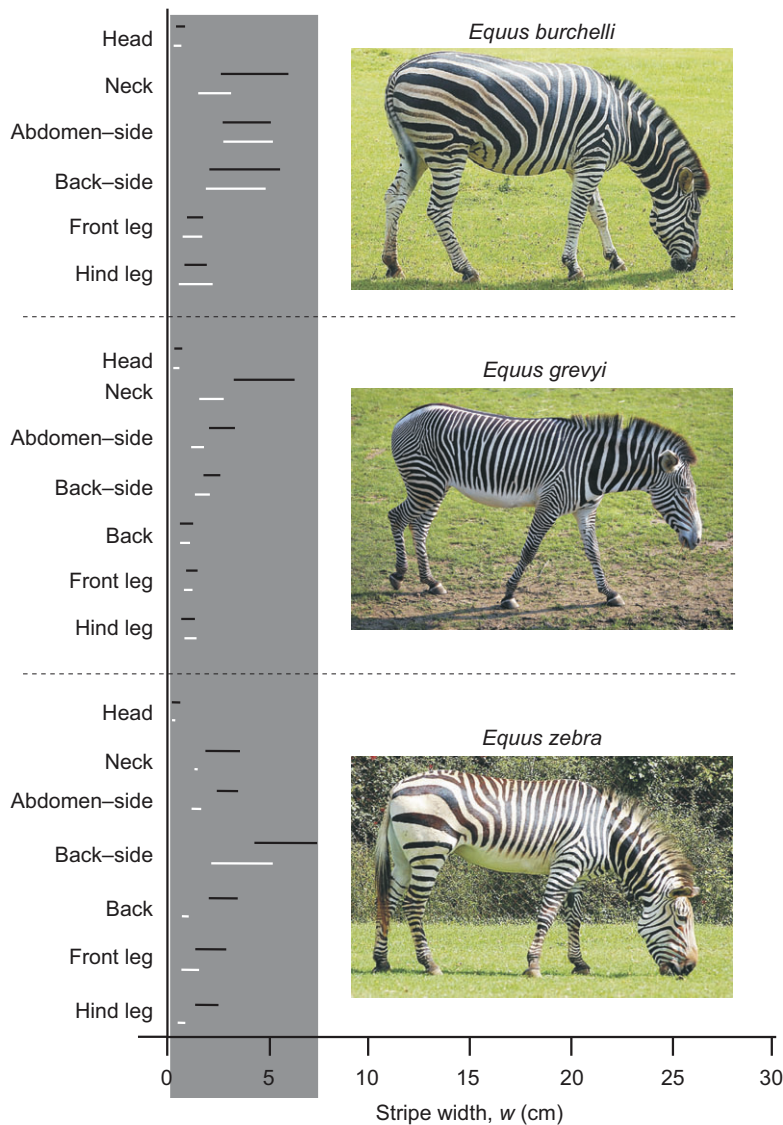


Fig. 1. Photographs of the three extant zebra species: plains zebra, *Equus burchelli* (<http://www.shoarns.com/ZebraGallery.html>), Grevy's zebra, *E. grevyi* ([http://www.easypedia.gr/el/images/shared/4/48/Equus_grevyi_\(aka\).jpg](http://www.easypedia.gr/el/images/shared/4/48/Equus_grevyi_(aka).jpg)), and mountain zebra, *E. zebra* (<http://www.shoarns.com/ZebraGallery.html>). The horizontal black and white bars represent the ranges of the width (w) (mean \pm s.d. in cm) of the black and white stripes, respectively, measured on different body parts (head, neck, abdomen-side, back-side, back, front leg, hind leg) of *E. burchelli* (13 coats), *E. grevyi* (5 coats) and *E. zebra* (1 coat) (supplementary material Fig. S4). Vertical grey column: range of w ($0.23 \text{ cm} < w < 7.47 \text{ cm}$) measured on zebra coats (minimum of mean $-$ s.d. $\leq w \leq$ maximum of mean $+ \text{ s.d.}$).

($\chi^2=6.53$, d.f.=1, $P<0.01$), with the striped pattern capturing fewer individuals than the white one. The black and the brown horse models reflected highly polarized light ($d>80\%$) at and near the Brewster angle [θ_{Brewster} : at which the surface-reflected ray of light is perpendicular to the refracted one penetrating into plastic. $\theta_{\text{Brewster}}=\arctan(n)=56.3$ deg from the vertical for the refractive index $n=1.5$ of plastic], while the white horse model reflected effectively unpolarized ($d<5\%$) light. The black and white stripes of the zebra model reflected light with high ($d>80\%$) and low ($d<5\%$) degrees of polarization, respectively. Seen from the side and the rear, certain parts of the black and brown horse models reflected highly polarized light [see fig. 4 of Horváth et al. (Horváth et al., 2010)], and thus these areas of the body surface were most attractive to polarotactic tabanids. In the case of the white horse model, there existed no such polarotactically attractive body parts, while small parts of the black stripes of the zebra model were also polarizationally attractive. These reflection-polarization characteristics partly explain the attractiveness of these horse models to polarotactic tabanids observed in experiment 4.

In experiment 5, the vertical sticky striped test surfaces Z13 and Z5, with $13 \times 4=52$ ($N=14$) and $5 \times 4=20$ ($N=13$) black stripes, trapped the least tabanids, the vertical grey ($N=29$) and white ($N=95$)

surfaces captured more flies, while the vertical striped surfaces Z2 and Z1, with $2 \times 4=8$ ($N=107$) and $1 \times 4=4$ ($N=467$) black stripes, caught the most tabanids (supplementary material Table S6). Using χ^2 test, there were significant differences in the number of tabanids trapped between the test surfaces Z5/Z13 and Grey, Grey and White, Z5/Z13 and Z2, and Z2 and Z1 (statistics are given in supplementary material Table S7). According to the one-way ANOVA test, there were significant differences between Z5/Z13 and Z2, Z2 and Z1 (supplementary material Table S7). According to the χ^2 -test, on surfaces Z2 and Z1, the black stripes trapped significantly more tabanids than the white stripes (supplementary material Table S8). Thus, only when the white and black stripes are wide enough is there a difference in the number of tabanids caught by the black and white stripes. This may be a matter of landing inaccuracy due to the narrow stripes: a tabanid may want to land on a black stripe, for example, but accidentally lands on a white one.

In experiment 6, the horizontal sticky test surface H-Z17+ (supplementary material Fig. S3B) trapped the least tabanid flies ($N=208$; 17.8% of total), the horizontal sticky test surface H-Z9+ (supplementary material Fig. S3C) captured more tabanids ($N=361$; 30.9%), while the horizontal test surface H-Z17_ (supplementary material Fig. S3A) caught the most tabanids ($N=600$; 51.3%; Fig. 3;

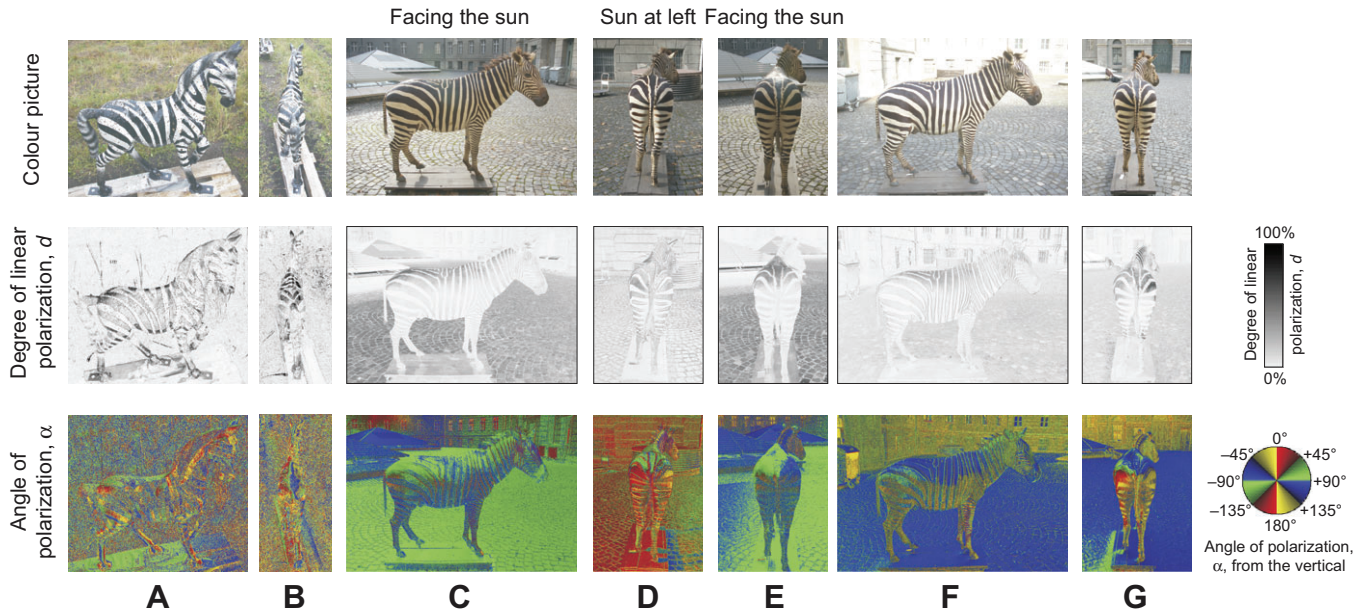


Fig. 2. Colour pictures (row 1), patterns of the degree of linear polarization, d (row 2) and angle of polarization, α (clockwise from the vertical) (row 3) of the zebra-striped sticky horse model used in experiment 4 and a real-size zebra model covered by an *Equus burchelli* coat measured by imaging polarimetry in the blue (450 nm) part of the spectrum from the side (A,C,F) and from behind (B,D,E,G). The optical axis of the polarimeter was -20 deg from the horizontal for A–B and 0 deg for C–G. The zebra models were sunlit (A–E) or shady (F,G). The polarimeter faced the sun (C,E) or the sun was to the left (A,D) or behind the polarimeter (B).

supplementary material Table S9). Similar results were obtained for the vertical sticky test surfaces V-Z17+ ($N=64$; 17.3%), V-Z9+ ($N=112$; 30.2%), V-Z17_ ($N=195$; 52.5%) used in experiment 6 (Fig. 3; supplementary material Table S9). There were significant differences in the numbers of tabanids trapped between the test surfaces H-Z17_ versus H-Z9+, H-Z9+ versus H-Z17+, V-Z17_ versus V-Z9+, V-Z9+ versus V-Z17+ (χ^2 test, $P < 0.001$ in all cases; supplementary material Tables S9, S10). According to the one-way ANOVA test, there were significant differences between H-Z17_, H-Z9+ and H-Z17+ as well as between V-Z17_, V-Z9+ and V-Z17+ (statistics given in supplementary material Tables S9, S10). From experiment 6, we conclude that (horizontal or vertical) stripes with the same brightness and colour but with alternating orthogonal directions of polarization are less attractive to tabanids than similar polarizing surfaces with homogeneous (constant) direction of polarization. Furthermore, similar to surfaces with black and white stripes, the attractiveness to tabanids of (horizontal or vertical) homogeneously coloured surfaces with alternating orthogonal directions of polarization decreases as the width of polarizing stripes decreases.

The reflection–polarization characteristics of the body surface of real zebras (e.g. *E. burchelli*) are practically the same as those of the zebra model used in experiment 4 (Fig. 2). Depending on the lighting conditions, the posture of zebras and the viewing direction relative to the sun, the black stripes on the back–side of zebras can reflect highly polarized light (Fig. 2C–G), which might be attractive to polarotactic tabanids if the polarizing black surface were not fragmented by unpolarizing white stripes.

Fig. 3 shows the number (N) of tabanids trapped by the test surfaces as a function of the widths (w) of the black and white stripes for our six experiments (supplementary material Fig. S4). The catch number N decreases monotonously with decreasing w . According to Fig. 3, horizontal, vertical or zebra-shaped striped surfaces with brightness

and/or polarization modulation have a negligible attractiveness to tabanids for stripe widths of $0.23 \text{ cm} < w < 7.47 \text{ cm}$ (represented by a vertical grey bar in Figs 1 and 3), which fall in the range of the mean stripe width in *E. burchelli*, *E. zebra* and *E. grevyi* zebras.

DISCUSSION

We have shown here that the evolution of stripes with brightness and/or polarization modulations disrupting the homogeneous pattern of reflected light might be a selective advantage in avoiding attacks from polarotactic tabanids. We conclude that zebras have evolved a coat pattern in which the stripes are narrow enough to ensure a minimum attractiveness to tabanid flies. Parasite infections have been shown to be involved in the evolution of sexual signals and colouration in animals (Hamilton and Zuk, 1982; Andersson, 1994), further stressing the potential link between the attacking parasite and the evolution of the host colouration as a response. There are many different hypotheses proposed to explain the possible benefits of zebra stripes (see Appendix and references therein). Although there is not necessarily one single mechanism to explain the selective advantage of these stripes, the majority of these hypotheses are presently unconvincing and suffer from lack of supporting experimental evidence (Ruxton, 2002; Caro, 2009). Here, we present the first experimentally supported explanation for the underlying mechanism for one of the possible advantages of zebra stripes. The reduced attractiveness to tabanids (and more generally of other biting insects, e.g. tsetse flies and mosquitoes) alone might not explain the striped coat pattern in zebras, but we demonstrate here its important role in parasite avoidance.

More than 4154 species of tabanid flies have so far been described and they are considered to be among the major dipteran pests of humans and animals worldwide (Krinsky, 1976; Foil, 1989). Despite this, the ecology and disease transmission of different tabanids are still not well investigated (Foil, 1989). Tabanids

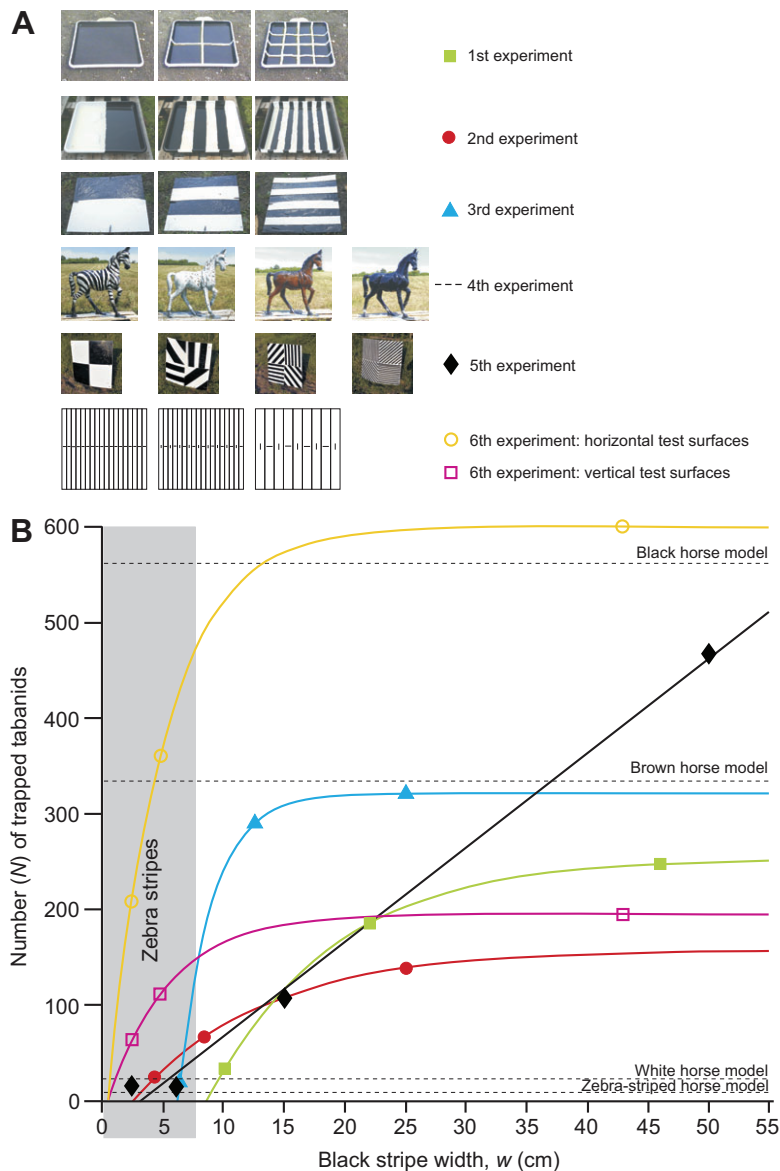


Fig. 3. (A) Stimuli used in the six experiments (details in the text). (B) Total number, N , of tabanids trapped by the sticky striped test surfaces in experiments 1–6 as a function of the width, w (cm), of the black and white stripes (experiments 1–5) and the linearly polarizing stripes (experiment 6). The continuous exponential curves pass through the corresponding three data points of experiments 1–3 and 6, while the straight line is fitted to the four data points of experiment 5 by means of the method of least-squares. The four horizontal broken lines show the numbers of tabanids captured by the sticky black, brown, white and zebra-striped horse models used in experiment 4. The vertical grey bar represents the range of w ($0.23 \text{ cm} < w < 7.47 \text{ cm}$) measured on zebra coats (minimum of mean – s.d. $\leq w \leq$ maximum of mean + s.d.). In experiment 5, the chequered test surface composed of two black squares and two white squares was considered as a pattern with a stripe width of $w=50 \text{ cm}$.

transmit severe pathogens to their hosts (Foil, 1989; Hall et al., 1998), and the transmission of diseases may be facilitated in large flocks of grazing mammals, where the distance between individuals is short (Foil, 1983). Thus, strong negative effects of tabanids are to be expected in open plains and savannahs in Africa, where grazing mammals are numerous. The animal hosts of tabanids may suffer high fitness costs, as several of the diseases transmitted by blood-sucking dipterans have lethal effects on the hosts (Foil, 1989; Hall et al., 1998). In addition, the biting of tabanids may prevent the animals from grazing in exposed areas or during certain parts of the day, as they have to seek shelter in the shade to escape from the attacks (Horváth et al., 2010), resulting in reduction of body mass and milk production (Hunter and Moorhouse, 1976; Harris et al., 1987; Lehane, 2005). Parasites have been shown to be a strong selective agent in mammals and birds and may lead to the evolution of exaggerated traits such as antlers in gazelles and deer as well as bright and elongated plumage characteristics in birds (e.g. Hamilton and Zuk, 1982; Andersson, 1994). Sexual selection and mate choice might drive this gradual change of morphology and plumage characteristics to extreme forms (Andersson, 1994). However, one may also expect immunological, morphological or behavioural

adaptations to evolve in order to avoid parasite attacks and prevent disease transmission in host animals. In an arms race between the parasite and host, one way to escape from being exposed to parasites would be to manipulate the signal by which the parasite is finding its host, e.g. odour or vision. As we have shown in this work, in the case of tabanid flies (using vision and odours to find hosts), an efficient way to escape attacks is to disrupt the reflected polarized signal that is used by tabanids in host location. The selection may act differently on birds and mammals, depending on the structure of their feathers and fur.

If a tabanid fly with a given spatial resolution of its compound eyes flies towards a zebra, from a remote distance it cannot yet perceive the zebra stripes. Thus, the attractiveness of the zebra is obviously determined only by the average brightness of the zebra coat. As the tabanid approaches the zebra and reaches a critical threshold range, its eyes begin to recognize the zebra stripes. Only within this critical distance are the stripes effective to influence the visual attractiveness to tabanids. The higher the visual acuity of tabanid eyes (i.e. the smaller and/or more numerous the corneal lenses), the larger is this critical range at which the stripes are advantageous not to attract tabanid flies.

In our experiments 1–5, polarization was confounded with brightness, because black and white stripes offer both polarization and brightness modulations. However, the results of experiment 6, using isoluminant stripes varying only in the direction of polarization, showed the important role of polarization in the reduced attractiveness of striped patterns to polarotactic tabanids. Although on the basis of our results the relative contributions (in %) of brightness and polarization modulations to the small attractiveness of zebra stripes to tabanids cannot be determined, they surely interact, because black and white stripes possess both brightness and polarization modulations. Nevertheless, experiment 6 demonstrates well the strong contribution of polarization modulation, since in this experiment there were, in practice, only polarization contrasts between the neighbouring stripes.

In experiment 5, the vertical grey test surface was less attractive to tabanids than the white test surface and the striped surface Z1, while it was more attractive than the striped surfaces Z5 and Z13 (supplementary material Table S6). From this, it is clear that the investigated tabanids were attracted or not attracted to the vertical striped surfaces by the stripes themselves, rather than simply due to the average brightness of these surfaces. Previously, Kriska et al. tested five salad-oil-filled horizontal trays with different greyness ranging from white (100%), light grey (25%), medium grey (50%), dark grey (75%) and black (0%) (Kriska et al., 2009). They found that the darker the grey, the larger was its attractiveness to tabanids because the higher was the degree of linear polarization of horizontally polarized reflected light. This is the typical positive polarotaxis governed by the polarization characteristics rather than the brightness of reflected light. Vertical surfaces reflect horizontally polarized light only if they are seen from certain directions of view, if the plane of reflection is vertical (the direction of polarization of reflected light is always perpendicular to the reflection plane). Depending on the viewing direction, in experiment 5, the vertical grey test surface reflected horizontally, obliquely or vertically polarized light with low degrees of polarization ($d < 25\%$), while the vertical white test surface reflected virtually unpolarized light ($d < 5\%$). Thus, the larger attractiveness of the vertical white surface relative to that of the vertical grey surface demonstrates that, in the host choice of tabanids, brightness also plays an important role, in addition to polarization. However, in experiment 5, the decrease in attractiveness to tabanids of striped vertical test surfaces (with the same, 50% average greyness) with decreasing stripe width further supports our conclusion that, in experiments 1–6, the stripe width was the relevant control parameter.

One possible function of zebra stripes may be protection from tsetse flies (Harris, 1930; Waage, 1981; Gibson, 1992). Tsetse flies avoid striped surfaces and congregate on solid objects (Vale, 1974). They usually need a large, plainly coloured subject to see and land on; therefore, they do not bite zebras as often as other, homogeneously coloured animals (Estes, 1992). Our results are more than a modification of this old tsetse fly hypothesis (Turner and Invest, 1973; Waage, 1981; Brady and Shereni, 1988; Gibson, 1992). We expanded the group of parasitic insects not attracted by striped patterns to the family of tabanid flies and our results have two aspects that distinguish them from the tsetse fly hypothesis.

(1) We revealed the behavioural and physical basis of the reduced attractiveness of striped patterns to tabanids. Previously, we showed that tabanids possess polarization vision to detect water by means of the horizontal polarization of light reflected from the water surface (Horváth et al., 2008). Tabanids also have positive polarotaxis, i.e. are attracted to linearly polarized light, which also partly governs their host choice (Horváth et al., 2010). This

polarotaxis is progressively disrupted by a black-and-white stripe pattern on the body surface of the host animal as the stripe width decreases. More importantly, the attractiveness of striped patterns to polarotactic tabanids is considerably reduced even if the stripes can be sensed only in the polarization domain. We showed that homogeneously coloured (dark grey) horizontal and vertical surfaces with stripes of alternating orthogonal directions of polarization are also less attractive than similar surfaces with constant polarization. This demonstrates the important role of polarization in the small attractiveness of striped patterns to tabanids. Note that in the case of zebra coats, brightness differences are inevitably associated with polarization differences: the white stripes reflect weakly polarized light while the black stripes polarize light strongly, and the directions of polarization of light reflected from the white and black stripes are also different. These brightness and polarization differences of zebra-striped patterns synergistically reduce the attractiveness to polarotactic tabanids.

(2) We also showed how the attractiveness of striped patterns to tabanid flies decreases with decreasing stripe width. It is an important advance that we could show that the stripe width of all three extant zebra species (*E. zebra*, *E. burchelli* and *E. grevyi*) is nearly in that range, where the attractiveness to tabanids is minimal (Fig. 3). In the experiments conducted with tsetse flies and striped test surfaces (Turner and Invest, 1973; Waage, 1981; Brady and Shereni, 1988; Gibson, 1992), stripe width was not assessed.

Our field experiments were performed in Hungary, and consequently only some Hungarian tabanid species were involved (see Materials and methods and supplementary material Tables S2, S4). Our results are, however, more general, and are in all probability valid also for African tabanid species living in the distribution areas of zebras; African tabanids should also be polarotactic, as insects associated with water generally are (Schwind, 1991; Schwind, 1995; Wildermuth, 1998) because their larvae develop in water or mud (Kingdon, 1979; Moss, 1982; Leclercq and Maldes, 1987; Churcher, 1993; Leclercq, 2000; Tegegne, 2004). Compared with more temperate regions (Chvala et al., 1972), the African tabanid fauna is much richer in number of species present, and the distribution ranges cover most of the continent (Surcouf and Ricardo, 1909; Leclercq, 1954; Uscher, 1972; Leclercq and Maldes, 1987), suggesting that the selection pressure for striped coat patterns as a response to attacking blood-sucking dipteran parasites is probably high in this region.

Real zebras have a very strong odour and breathe out CO₂. In the field, odours of zebras, horses and other mammals surely play a role in the host choice by tabanids (Hall et al., 1998; Lehane, 2005). It is conceivably possible that the odour and CO₂ are attractive to tabanids and may overwhelm the small visual attractiveness of the striped coat pattern. It could be experimentally tested in the future whether odour either combines or perhaps even overrides the visual attractiveness, especially the polarotactic effect in tabanids. For tsetse flies, for example, it was shown that odour changes the attractiveness of colour (Hariyama and Saini, 2000). But tsetse flies are not tabanids and do not need water for their larvae to develop in, and they might therefore respond differently from tabanids. The odour, CO₂ and non-zero visual attractiveness of the striped coat of zebras could be the major reasons for zebras sometimes suffering from blood-sucking tabanids.

In all six experiments, we used essentially the same method: several test surfaces (oil-filled trays, sticky two-dimensional surfaces and sticky three-dimensional horse models) with different reflection–polarization characteristics trapped tabanids, which were counted and removed periodically. After tabanid counting, the order

of test surfaces was randomly changed. Since the captured tabanids and other non-tabanid insects were removed, the new arrivals were not influenced by the presence of insect carcasses; furthermore, the experimental situation was altered by the random changing of test surfaces. Thus, after tabanid counting, a new replication of each experiment began. In our experiments, the number of replications (R) and the number of days (D) of the whole experiment were as follows: experiment 1, $R=9$, $D=18$; experiment 2, $R=13$, $D=67$; experiment 3, $R=9$, $D=28$; experiment 4, $R=27$, $D=59$; experiment 5, $R=5$, $D=42$; experiment 6, $R=24$, $D=68$. According to statistical analyses, these numbers of replications were large enough to detect significant differences.

All three zebra species have the narrowest stripes and the thinnest skin on their head and legs (Figs 1, 2, supplementary material Fig. S4), where the stripe widths are so small that they effectively do not attract tabanid flies (Fig. 3). This phenomenon may reflect an evolutionary adaptation. In the head, there are several sensory organs (eyes, ears, tongue, muzzle), the efficient functioning of which is most important for survival. The legs also are indispensable to escape from predators. Consequently, head and legs must be protected in the best possible way from blood-sucking parasites (e.g. tabanid and tsetse flies), since any injury to these body parts due to aggressive biting insects might result in their insufficient functioning, undermining the escape and survival of the animal. Furthermore, in the head and legs, the blood vessels can more easily be reached through the thin hide, and a more efficient protection is therefore urgently needed for these body parts. We suggest that the numerous narrow stripes on the head and legs of zebras may serve such a visual protection.

Zebra stripes might also make it difficult for tabanid flies to be camouflaged when sitting on the host. Tabanids are usually dark brown or grey, with different brightness and colour patterns. These characteristics are advantageous when they land on dark-coated host animals because they can be more difficult to detect visually by insectivorous birds, which often follow larger herbivores, the major host animals of tabanids. However, this camouflage of tabanids is likely to be inefficient when they land on a zebra coat, due to the large and spatially frequent brightness and colour contrasts between the tabanid body and the underlying black or white coat.

Further research should explain why the predecessors of Eurasian horses were apparently striped but, through evolution, have lost almost all of their stripes despite the fact that they occur in tabanid-infested regions. Thus, another evolutionary enigma is why Eurasian horses have not kept the stripes, given that they would reduce attacks by tabanid biting flies. After all, African horses, namely zebras, kept their stripes. Sometimes domestic horses and donkeys express stripes on their bodies, which conspecifics apparently suppress. These are the so-called throw-backs of domestic animals (Gould, 1983).

APPENDIX

Zebra stripes and their possible functions

The stripes of zebras are nearly vertical on the head, neck and trunk, while approximately horizontal on the back-side and legs. Zebras occur in Central and South Africa, where three species are found. (1) Most common is the plains zebra, *Equus burchelli* (with 12 subspecies), distributed across extensive parts of southern and eastern Africa. It has approximately 26 wide caudal stripes per side, some of which extend towards the belly at the rear of the animal (Fig. 1). (2) Grevy's zebra, *E. grevyi*, is the largest species (Fig. 1), having about 80 stripes on each side perpendicular to the long axis

of its body. It is an inhabitant of the semi-arid grasslands of Ethiopia and northern Kenya. (3) The mountain zebra, *E. zebra*, having two subspecies, is found in southwest Africa and has approximately 55 stripes on each side, with three horizontal bands near the hind legs and a white belly (Fig. 1). The now extinct quagga, *E. quagga*, also had a partially striped coat pattern most pronounced in the front part of the body, on the head, neck and front half of the body [plate I in Bard (Bard, 1977)].

Several different hypotheses have been proposed to explain the possible functions and evolutionary significance of the black-and-white striped coat pattern in zebras. The alternative hypotheses and their explanations have been discussed in recent reviews (Ruxton, 2002; Caro, 2009).

Apparent size increase. The stripes may create a visual illusion that increases the apparent size of the zebra. This illusion could afford zebras an advantage over their predators (Cott, 1966; Cloudsley-Thompson, 1984; Vaughan, 1986; Morris, 1990).

Visibility in poor light. In low light conditions (near dusk and dawn, or in moonlight), the stripes might be difficult to make out even from a close distance (Galton, 1851; Kipling, 1908; Cott, 1966; Cloudsley-Thompson, 1984; McLeod, 1987; Morris, 1990).

Moving stripes may dazzle predators. The moving stripes of fleeing zebras might make it difficult for predators to single out an individual zebra from the herd (Cott, 1957; Kruuk, 1972; Eltringham, 1979). The stripes of even a single individual may be enough to dazzle and confuse a predator (Morris, 1990).

Camouflage. The stripes may allow zebras to blend in with their background (e.g. tall grass or savannah vegetation) by dissolution of their contour (Wallace, 1867; Wallace, 1879; Thayer, 1909; Marler and Hamilton, 1968). The most vulnerable juveniles and female adults of several, non-striped ungulate species also have a camouflaging striped coat.

Social benefits. Since the stripe pattern is individual, as a fingerprint, zebras may recognize each other on the basis of their stripes (Morris, 1990; Prothero and Schoch, 2003). This might be especially important in the visual communication between mothers and their foals or in reinforcing the bond between male and female in courtship (Cloudsley-Thompson, 1984; Becker and Ginsberg, 1990). Stripes might also be visual markers for group bonding or to direct companions to particular parts of the body for grooming (Kingdon, 1984).

Fitness indication. Irregularities in the stripe pattern due to disease, injuries or any kind of acute dysfunction might be a visual signal about the poor physical condition (fitness) of the individual for mate-seeking zebras (Ruxton, 2002).

Thermoregulation. The fat pattern in the skin may correlate with the pattern of black stripes, which might function as heat absorbers, and thus may play a role in the thermoregulation of the body. Furthermore, the black and white stripes may work together (inducing rotary breezes by thermal convection of air) to keep the animal cooler than without stripes (Cloudsley-Thompson, 1984; Kingdon, 1984; Morris, 1990; Louw, 1993).

Protection from tsetse flies. Zebras seem to be unfavoured hosts for tsetse flies (Jordan, 1986). According to Harris (Harris, 1930), Waage (Waage, 1981) and Gibson (Gibson, 1992), the purpose of zebra stripes may be protection from tsetse flies, which are vectors of dangerous pathogens, especially the trypanosomes of nagana and sleeping sickness (Foil, 1989). Tsetse flies avoid striped surfaces and congregate on solid objects (Vale, 1974). They usually need a large, plainly coloured subject to see and land on; therefore, they do not bite zebras as often as other, homogeneously coloured animals (Estes, 1992).

These explanations have been thoroughly discussed and criticized by Ruxton (Ruxton, 2002), who concluded that the majority of these hypotheses are experimentally unconfirmed, and thus the exact cause of stripes in zebra remain unknown. Caro also recently discussed some of the alternative hypotheses proposed to explain the striped pattern, ending up with the same conclusion – that the reason for the evolution of a striped coat in zebras is still unknown (Caro, 2009).

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