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Stripes disrupt odour attractiveness to biting horseflies: Battle between ammonia, CO_2, and colour pattern for dominance in the sensory systems of host-seeking tabanids

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HIGHLIGHTS

- Blood-sucking female tabanids search for host animals by visual and olfactory cues.
- Striped coat patterns are visually less attractive to tabanids than homogeneous targets.
- Tabanids are strongly attracted by CO2 and ammonia emitted by their hosts.
- In experiments we found that the poor visual attractivity of stripes to tabanids is not overcome by olfactory attractiveness.
- This demonstrates the visual protection of striped patterns against tabanids transmitting lethal diseases to ungulates.

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ABSTRACT

As with mosquitoes, female tabanid flies search for mammalian hosts by visual and olfactory cues, because they require a blood meal before being able to produce and lay eggs. Polarotactic tabanid flies find striped or spotted patterns with intensity and/or polarisation modulation visually less attractive than homogeneous white, brown or black targets. Thus, this reduced optical attractiveness to tabanids can be one of the functions of striped or spotty coat patterns in ungulates. Ungulates emit CO_2 via their breath, while ammonia originates from their decaying urine. As host-seeking female tabanids are strongly attracted to CO_2 and ammonia, the question arises whether the poor visual attractiveness of stripes and spots to tabanids is or is not overcome by olfactory attractiveness. To answer this question we performed two field experiments in which the attractiveness to tabanid flies of homogeneous white, black and black-and-white striped three-dimensional targets (spheres and cylinders) and horse models provided with CO_2 and ammonia was studied. Since tabanids are positively polarotactic, i.e. attracted to strongly and linearly polarised light, we measured the reflection–polarisation patterns of the test surfaces and demonstrated that these patterns were practically the same as those of real horses and zebras. We show here that striped targets are significantly less attractive to host-seeking female tabanids than homogeneous white or black targets, even when they emit tabanid-luring CO_2 and ammonia. Although CO_2 and ammonia increased the number of attracted tabanids, these chemicals did not overcome the weak visual attractiveness of stripes to host-seeking female tabanids. This result demonstrates the visual protection of striped coat patterns against attacks from blood-sucking dipterans, such as horseflies, known to transmit lethal diseases to ungulates.

1. Introduction

Female tabanid flies searching for blood nourishments are attracted to their host animals by the odours, shape, movement, brightness and colour of the host [1,2,19,20,30,33,34,39], and also by the linear polarisation of host-reflected light [3,9,10,17,18,23]. Tabanids wait for hosts to appear in shady areas under bushes and trees [37]. Sight is the main host finding mechanism, but body temperature (warmth) and odour (mainly ammonia, carbon dioxide and sweat) also play an important role [31,35]. Moving objects, especially if dark coloured, are most prone to be attacked by tabanids [4,36].

Tabanids are intermittent feeders: their painful bites generally elicit a protective response from the victim so they are frequently forced to move to another host without having the chance to procure a full blood meal. Consequently, they may serve as mechanical vectors

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of some diseases and/or parasites, e.g. anthrax, tularemia, anaplasmosis, hog cholera, equine infectious anaemia, filariasis and Lyme disease transmitted by their bites [11,25,26]. A serious problem can occur in mammals when the blood loss is high due to abundant tabanid bites, i.e. hosts exposed to frequent bites can lose up to 0.5 ml of blood per fly [12], which can severely weaken or even kill them. Thus, numerous painful bites from high populations of tabanids can reduce the fitness of the host animals. Furthermore, tabanids sometimes irritate ungulates so seriously that these host animals cannot graze [24]. Consequently, host animals exposed to tabanids, show strong behavioural responses, such as escape behaviours when approaching flights of tabanid flies are heard. Thus, evolution of a coat pattern with a weak attractiveness to tabanids could be an important selective advantage to mammalian hosts.

Water-seeking male and female tabanid flies are attracted to horizontally polarised light reflected from a water surface [17,23]. Host-seeking female tabanids, using blood as nourishment to increase clutch size and to develop and ripen their eggs, are also attracted to linearly polarised light reflected from the coat of host animals, independent of the direction of polarisation [9,18]. Recently, it was shown that polarotactic tabanids find striped or spotted patterns with intensity alteration (alternating dark and bright stripes or patches) and/or polarisation modulation (stripes or patches with alternating orthogonal directions of polarisation) much less attractive than homogeneous white, grey, brown or black targets. This may be one of the functions of zebra stripes [7,10,32] and spotty animal coats [3]. The attractiveness to tabanids diminishes with decreasing stripe width and spot size. Stripes narrower than a critical width ($\approx$5 cm, [10]) and spots smaller than a threshold size (diameter $\approx$ 10 cm, [3]) are effective enough not to attract tabanids. Ref. [10] demonstrated that stripe widths on the coats of all three extant zebra species (*Equus burchelli*, *Equus grevyi*, *Equus zebra*) fall in a range where the striped pattern is most disruptive, i.e. least attractive to host-seeking tabanids.

Similarly to other ungulates, zebras emit carbon dioxide (CO_2) via their breath and ammonia associated with their urine (ammonia originates from the decay of urine). Tabanid flies are attracted by CO_2 and ammonia, and these chemical attractants are therefore frequently used in tabanid traps (e.g., [13,19,24,28,29,39]). Thus, the question arises whether the weak optical attractiveness of the striped coat pattern of zebras to tabanids can be overcome by the olfactory attractiveness of zebras to tabanids. Could an attractive zebra smell (CO_2, ammonia, sweat) compensate for the poor visual attractiveness of a striped pattern to tabanids, resulting in the loss of the selective advantage of striped coat patterns?

To answer this question, we performed two field experiments, in which we studied the attractiveness to tabanid flies of sticky homogeneous white, black and black-and-white striped three-dimensional targets and horse models provided with CO_2 and ammonia. Since tabanids have positive polarotaxis, we measured the reflection–polarisation characteristics of the test targets used in our experiments.

2. Materials and methods

Experiment 1 was performed between 21 June and 12 September 2012 on a Hungarian horse farm in Szokolya (47° 52′ N, 19° 00′ E) to investigate the influence of ammonia (the most typical component of bacterially decaying urine) on the attractiveness of sticky three-dimensional visual targets with different surface patterns to tabanid flies. Each target was composed of a sphere (diameter = 50 cm, Fig. 1A–C) and two cylinders (height = 50 cm, the major and minor axis of the elliptical cross-section was 50 cm and 30 cm, respectively, Fig. 1D–F) imitating rounded (spherical) or elongated (cylindrical) body parts of a host animal for host-seeking female tabanids. There were two identical target groups. Each target group was composed of a white, a black-and-white striped and a black target arranged 5 m apart along a straight line (Fig. 1G, H). The homogeneous black and white spheres were common inflatable beach balls sprayed by black and white paint, respectively. The striped sphere was a black-sprayed beach ball onto which white plastic stripes (width = 2 cm) were fixed with adhesive. The cylinders were composed of white plastic buckets. The black cylinders were produced by spraying the white buckets with black paint. The striped cylinders were made with painting black stripes (width = 4 cm) onto the white buckets. Each sphere was fixed at a height of 100 cm to a vertical metal rod stuck into the ground. Two cylinders with the same pattern (white, striped, or black) were impaled onto a vertical metal rod stuck into the ground 50 cm apart from the sphere with the same pattern (white, striped, or black). The height of the lower and higher cylinder was 50 and 100 cm from the ground, respectively. Since the sphere and the two cylinders with the same surface pattern (white, striped, or black) were quite close (50 cm) to each other, they might have been considered by host-seeking flying tabanids to belong to the same (host-imitating) target, thus the numbers of tabanids caught by the spheres and cylinders with the same pattern were pooled (Tables 1, 2). In both target groups all three different targets (white, striped, black) were presented simultaneously (Fig. 1G, H).

One target group was baited with ammonia, while the other group was unbaited. The two target groups were positioned 500 m apart (separation of the odour treatments) at two opposite sides of a grove in such

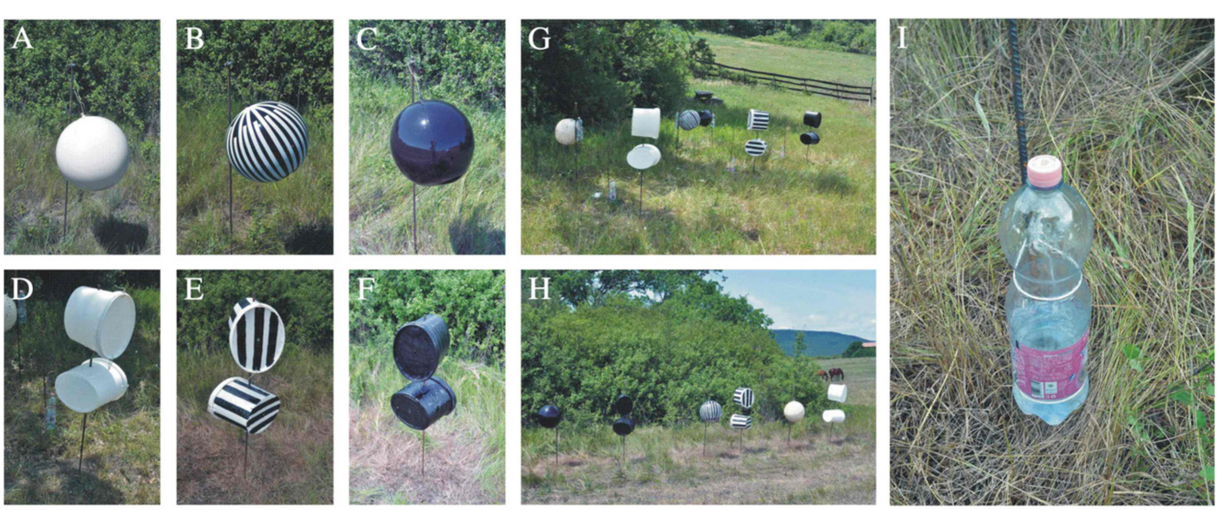

Fig. 1. Sticky white (A, D), black-and-white striped (B, E), and black (C, F) spheres (A–C) and cylinders (D–F) used in experiment 1. Arrangement of the sticky test targets with (G) and without (H) ammonia. (I) A plastic bottle with five small holes on its stopper containing aqueous ammonia as an ammonia source.