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Biting flies and zebra stripes

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Abstract

In all probability, biting flies are the evolutionary force that has shaped zebras' extraordinary coat coloration but there are a number of questions raised by this contention which we address in this review. We divide our discussion into (i) which groups of biting flies are thwarted by contrasting black and white striping; the variety of ways in which stripes might interfere with normal landing behaviour of flies; (ii) the ecological assumptions underlying fly-zebra sympatry; and (iii) the zebra diseases for which flies are vectors. We note that tabanid species differ in their landing sites on equids and that glossinids may not be affected by the stripes in the same ways as tabanids. We argue that aliasing or disruption of the targeting system are possible candidates for thwarting tabanid landing behaviour but that disruption of the aperture effect is not responsible. We show that tabanid and glossinid distributions closely overlap those of zebra species at a geographic and microhabitat scale, and that flies can carry several diseases fatal to zebras. We suggest that future research be targeted at the mechanism by which stripes thwart proper landing performance and identify which diseases and which carriers most impact zebras.

Reasons that zebras are striped

The unusual and striking coloration pattern of the three species of extant zebra (*Equus* sp) has generated many functional explanations over the last 150 years (Ruxton, 2002; Caro, 2020). Evidence for and against them can be condensed into four principal topics. (i) Stripes being a form of crypsis against predators have now been dismissed on grounds that lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) are only able to resolve stripes very close up (Melin et al., 2016); moreover, experiments show that zebra stripes are highly visible to human observers at all distances (Caro, 2016; Muhl-Richardson et al., 2021). (ii) Stripes confusing predators are unlikely to work because plains zebras (*Equus quagga*) do not bunch together during flights which could make one individual difficult to follow, or obscure its outline of individual animals, and they do not cause lions to misdirect their attack (Caro, 2016). Most damning, lions kill zebras more than expected from their abundance across 40 study sites in Africa (Hayward and Kerley, 2005) suggesting that confusion is a poor antipredator defence strategy. (iii) A third theme, that black and white stripes have different heat signatures (Cobb and Cobb, 2019) which set up convection currents that cool

zebras could only operate under very restricted circumstances: over the animal's dorsum, not over its flank or legs, and, problematically, not under breezy conditions or when the animal moves, as these would negate convection currents acting anywhere on the body (Caro, 2016; Pereszlényi et al., 2021). Moreover, experimental tests reveal no cooling benefits associated with striped objects or striped pelts (Horváth et al., 2018). (iv) In contrast to these ideas, stripes are an established potent force in reducing landings of biting flies based on experimental studies with striped artificial targets (Waage, 1981; Brady and Shereni, 1988; Gibson, 1992; Sasaki et al., 2020), horse models (Egri et al., 2012a), human models (Horváth et al., 2019), painted cows (Kojima et al., 2019), comparisons of live plains zebras with domestic horses (Caro et al., 2019; How et al., 2020), and the distribution of tabanid abundance corresponding to that of striped equids in the Old World (Caro et al., 2014).

The purpose of this chapter is to (i) examine the idea that biting fly taxa drive striping in zebras, (ii) critically explore the mechanisms underlying the effects of stripes on biting fly behavior, and (iii) reexamine the ecological assumptions that underlying biting flies being an important evolutionary force shaping equid morphology.

How generalizable are the biting fly findings?

The biting flies referred to in this chapter are all dipterans. Tabanidae comprise three subfamilies, the Tabadinae and Pangoniinae (horse flies), and the Chrysopsinae (deer flies) and consist of over 3000 species found all over the world except at the poles and some oceanic islands. The 31 species of Glossinidae are all in a single genus, *Glossina*, and are confined to sub-saharan Africa. Muscidae, consisting of over 4000 species of house flies and stable flies, have a worldwide distribution; one subfamily, the Muscinae, contains the genus *Stomoxys*. All species are a nuisance for equids.

The significance of striping as an anti-biting fly strategy was brought to attention forty years ago by Waage (1981) although it had been presaged by Harris (1930) and Barrass (1960). In the field, Waage set up stationary and moving experimental cylindrical models painted with alternating 5cm wide black and white stripes and control black or white cylinders. He recorded the number of flies electrocuted on the model and on a 1m² electrocuted unpainted screen next to it. Significantly more tsetse flies, principally *Glossina pallidipes* but also *G. morsitans* landed on the black or white models than on the striped models; tabanids were also recorded but there were insufficient numbers by themselves to draw statistical conclusions. Brady and Shereni (1988), working in the laboratory with satiated *Glossina morsitans* and *Stomoxys calcitrans*, found that flies preferred to land on black than on striped targets and that *Glossina* preferred thicker (7.5cm) over thinner (3.0cm) stripes. Gibson (1992), working in the field, presented *G. pallidipes* and *G. morsitans* with cloths of different colours and found that grey and both vertically and horizontally striped targets were less attractive than black or white targets. Finally, Egri and colleagues (2012a) working in the field with several species of European tabanids found that flies were least attracted to oil-filled black salad trays with more and thinner white stripes, and replicated these findings using sticky boards and half-sized horse models. These species included *Tabanus tergstinus*, *T. bromius*, *T. bovinus*, *T. autumnalis*, *T. miki*, *Atylotus loewianus*, *Haematopota italica*, as well as *Stomoxys calcitrans*; interestingly there appeared to be variation in the extent to which different species avoided striped targets over unstriped ones even within genera, with some *Atylotus loewianus* avoiding stripes but *A. fulvus* little affected (Table 1a); stripes seemed to affect *A. loewianus* particularly strongly in both of their experiments involving different numbers of stripes (Tables 1a and 1b).

Table 1. Numbers and proportions of females (the blood-feeding sex) and total tabanid flies of different European species avoiding black oil filled trays painted with different numbers of 2-cm wide stripes in Egri et al 2012a (from their Tables S2 and S4).

a) Experiment 1 from Egri et al (2012a)

Species	Tray	Female	Male	Total
<i>Tabanus tergstinus</i>	0 white stripes	102	37	139
	2 white stripes	84	36	120
	6 white stripes	13	3	16
	% avoiding stripes	51.3%		50.5%
<i>Tabanus bromius</i>	0 white stripes	60	0	60
	2 white stripes	37	1	38
	6 white stripes	8	1	9
	% avoiding stripes	57.1%		56.1%
<i>Tabanus bovinus</i>	0 white stripes	8	4	12
	2 white stripes	0	1	1
	6 white stripes	1	0	1
	% avoiding stripes	88.9%		85.7%
<i>Atylotus fulvus</i>	0 white stripes	1	0	1
	2 white stripes	6	0	6
	6 white stripes	4	0	4
	% avoiding stripes	9.1%		9.1%
<i>Atylotus loewianus</i>	0 white stripes	26	5	31
	2 white stripes	7	2	9
	6 white stripes	1	1	2
	% avoiding stripes	76.5%		73.8%

b) Experiment 2 from Egri et al (2012)

Species	Tray	Female	Male	Total
<i>Tabanus tergstinus</i>	0 white stripes	63	26	89
	2 white stripes	67	24	91
	6 white stripes	32	9	41
	12 white stripes	17	7	24
	% avoiding stripes	35.2%		36.3%
<i>Tabanus bromius</i>	0 white stripes	2	0	2
	2 white stripes	6	1	7
	6 white stripes	0	0	0
	12 white stripes	0	0	0
	% avoiding stripes	25.0%		22.2%
<i>Atylotus loewianus</i>	0 white stripes	33	4	37
	2 white stripes	20	3	23
	6 white stripes	1	0	1
	12 white stripes	0	0	0
	% avoiding stripes	61.1%		60.7%
<i>Haematotopa italica</i>	0 white stripes	5	8	13
	2 white stripes	5	10	15
	6 white stripes	2	9	11
	12 white stripes	0	0	0
	% avoiding stripes	41.7%		33.3%

While the above studies that focused on glossinids found strong effects of striping, it is noteworthy that Caro and colleagues (2014) found that intensities of striping on different parts of the body across 20 subspecies of zebra, wild asses and horses are not associated with the distribution of tsetse flies, although they are with tabanid abundances. Only the number of belly stripes is found to correlate with tsetse fly distribution in this broad comparative analysis (see also Larison et al., 2015). Lumping tabanids and glossinids together as being the driver of striping in zebras might therefore be overly simplistic.

While the four pioneering experimental studies point towards a relationship between biting diptera and zebra striping, they suffer from the fact that experimental designs differed, that flies were satiated in one study, some studies had few replicates, and targets may not reflect light in the same way as zebra pelts (Caro, 2016). Together, however, they provide convincing evidence that two species of glossinids, several species of tabanids, and possibly one species of *Stomoxys* eschew landing on stripes in experimental circumstances. This raises the possibility that stripes are a way of deterring all three dipteran groups from landing, and potentially muscidae, simuliidae and cuculidae although these have not been examined.

A second, more subtle issue is that biting flies choose to land on different areas of the host's body. For example, tabanids prefer to land on the legs and belly of ungulates (Kangwagye, 1977; Hollander and Wright, 1980; Phelps and Holloway, 1990) but this can differ across tabanid species. This has been well documented for North American tabanids feeding on cattle where species with longer mouthparts can feed in areas with longer or thicker hair (Mullens and Gerhardt, 1979). Similar site-specific preferences are found for Australian tabanid species feeding on horses (Muzari et al., 2010). Our studies concerning horseflies landing on zebras and striped coats placed on horses in UK show similar patterns (Caro et al., 2019; How et al., 2020). In these studies, we observed *Haematopota pluvialis* primarily approaching the main body or coat of the animals, and only occasionally targeting the legs (fig. 1). For example, in our 2018 season in Somerset we counted the number and location of 7484 *H. pluvialis* landings or attempted landings on 22 horses wearing two unpatterned rugs (black and grey). We found an average of only 11.5% of such landings or attempts were on the naked legs (SD = 13.1%, N=44 coat-horses), with all others recorded on the rug or naked head. In 2020 at a different field-site in Dorset, and based on 10 videos, we recorded the behaviour of *Tabanus bromius*, which were present in large numbers later in the summer. We found that, in contrast to *H. pluvialis*, an average of 83% (SD = 15%; N=116 landings) of *T. bromius* landings or attempts were performed around the naked legs and bellies of horses. Site preferences are important because they affect the duration of feeding per landing due to the host's ability to dislodge the fly, and ease with which the fly can penetrate hair and skin (Muzari et al., 2010). Both of these will in turn influence the probability of disease transmission (see below).

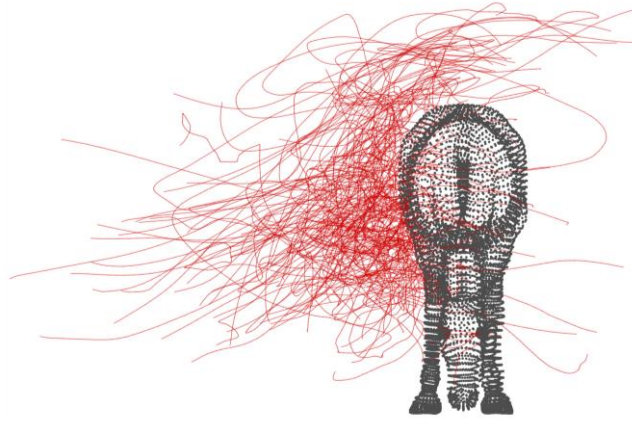


Figure 1. Tracking horseflies around targets. Trajectories of 107 horseflies (*Haematopota pluvialis*) approaching the flank of a domestic horse wearing a grey rug. (Redrawn from How et al. 2020).

Despite the conservative anatomy of the dipteran eye and its use for visually guided landing (Baird et al., 2013), all these observations suggest that some species of tabanids are more important pests than others and may be more effective carriers of disease. And the comparative analysis suggests that the rules for tabanids and glossinids may also differ (Caro et al., 2014).

Underlying mechanisms by which stripes could exert effects on tabanids

Our tabanid work showed that horseflies approach domestic horses wearing striped rugs as often as the same horses covered with black or white rugs but that far fewer tabanids actually landed on horses with striped external appearances (Caro et al., 2019). Parallel observations revealed that tabanids failed to decelerate when approaching zebras compared to horses and, anecdotally, flies were seen to bump into zebra pelage or fly past it. The mechanism by which stripes actually exert these effects is under investigation.

Aperture effect

One idea is that stripes interfere with optic flow (How and Zanker, 2014). Optic flow is the pattern of apparent movement of objects in the visual field caused by relative motion between an observer and the scene (fig 2a). As a fly approaches an object, the surface looms ever faster and the fly responds by reducing its speed to keep the rate of looming constant, resulting in a slow controlled landing (Baird et al., 2013). Even with a monochrome coat, there would have to be some (minimal) contrast on the coat to provide the optic flow that flies rely upon for executing smooth landings. Striped patterns could potentially disrupt landing behaviour by interfering with the radial symmetry of expanding optic flow fields (fig 2b). This is because, in the absence of other cues, moving stripes induce the strongest motion effects in directions perpendicular to stripe orientation, termed the aperture effect (Hildreth and Koch, 1987; Wuergler et al., 1996; Harris et al., 2000). Such disruption could prevent the fly from landing properly on a striped surface or landing at all if it usually relied on the radial symmetry of optic flow. By recording and reconstructing tabanid behaviour around horses wearing differently patterned coats, employing detailed video footage, we found that tabanids avoided landing on, flew faster near, and did not approach as close to striped and checked rugs compared to grey (How et al., 2020). Flies avoided checked

patterns in a similar way to stripes refuting the hypothesis that stripes disrupt optic flow via the aperture effect which critically demands parallel striped patterns to operate.

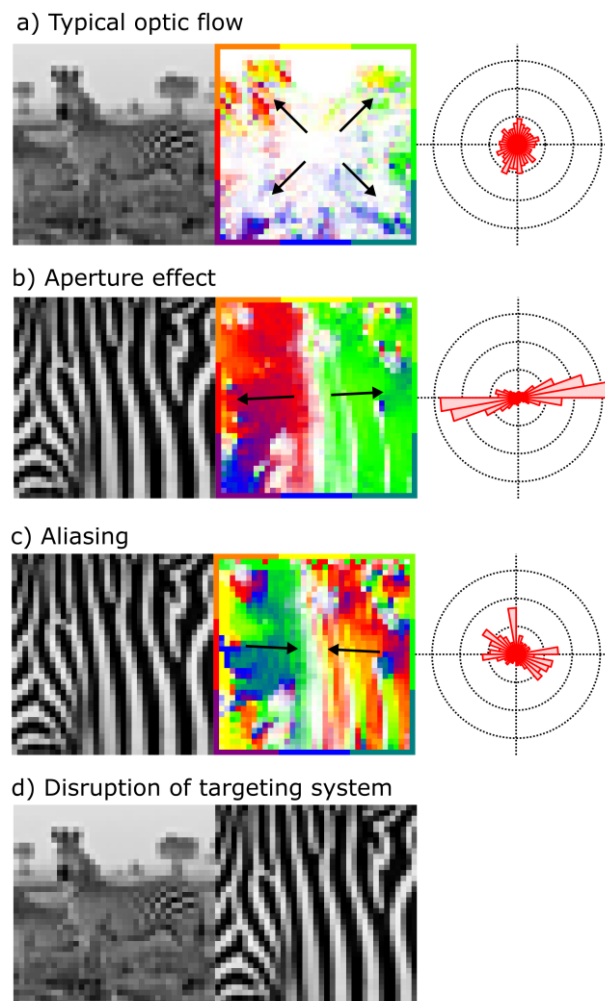


Figure 2. Possible mechanisms for the anti-biting fly properties of zebra stripes. a) Optic flow pattern typical of a non-striped scene. Left, still frame from scene. Middle, motion map with hue indicating direction (according to false-colour-coded frame) and saturation indicating strength. Right, polar histogram of motion-vector distribution showing the direction in which objects appear to be moving in the visual field. b) Aperture effect – striped scenes generate bimodal optic flow in directions perpendicular to stripe orientation. c) Aliasing – at certain speeds repetitive stripes are mismatched causing errors in motion detection. d) Targeting, a system independent of flight control, is disrupted by stripes when they come within visual resolution. (Adapted from How et al. 2020).

Aliasing

An alternative explanation is that a periodic pattern would be subject to spatial aliasing when it is viewed by an approaching insect's compound eye. When the (angular) period of stripes (λ) is larger than twice the interommatidial angle ($\Delta\phi$), the stripes would appear to expand across the visual field in the correct direction (i.e., producing optic flow that matches the angular expansion of the target surface). However, when λ is smaller than twice $\Delta\phi$ (which will occur when the insect is far away), stripes would appear to move in the opposite direction (Götz, 1965; How and Zanker, 2014; How et al., 2020). When the fly is very far away from the pattern, the pattern will appear grey because its (angular) spatial frequency is higher than the cutoff angular spatial frequency of the modulation transfer function (MTF) of

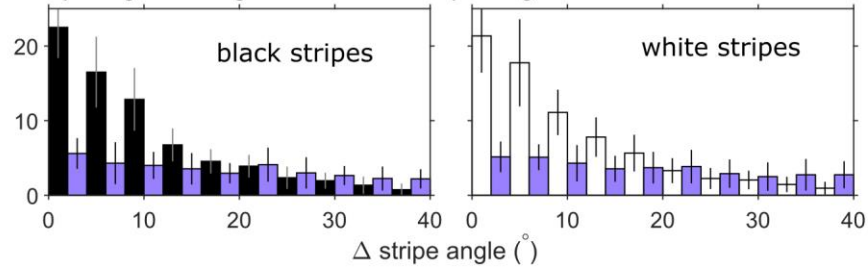
the visual system, which is determined by the width ($\Delta\rho$) of the angular acceptance function (the optics functions as a spatial low-pass filter) (see fig 2a left). As the fly approaches the pattern, the angular period of the pattern will progressively increase, and consequently the apparent contrast of the pattern will increase to the point where the pattern becomes visible (i.e., the contrast is suprathreshold). If the angular period of the pattern at this distance is smaller than twice the interommatidial angle, then spatial aliasing would occur and the apparent movement of the pattern would be in a direction opposite to that which would occur in a normal visual environment - which is dominated by low, non-aliasing spatial frequencies (fig 2c). This contradictory movement would work against the tendency for the fly to fixate the pattern, creating positive feedback and causing it to turn away from the pattern.

Key to this aliasing effect is that neighbouring stripes of the same colour should lie at a similar angle to each other and be of similar thicknesses because the process relies on mismatching repetitive elements of the pattern. To demonstrate that this is indeed the case with zebras, we examined photographs of 20 plains zebras taken in Katavi National Park, Tanzania in 2014. By measuring both the angle and thickness of black and white stripes along a transect bisecting the central part of the pattern, we noted that each stripe was more similar to its same-coloured neighbour than to a randomly assigned, same-coloured stripe from across the body (Fig 3a-c). We also compared the thickness of same-coloured neighbouring stripes with the nearest stripe of the opposite colour and noted that, despite opposite-coloured neighbouring stripes being adjacent, within-colour neighbours were more similar in width than between-colour neighbours in 18 out of 20 photographs (Fig 3d). Both of these measurements support the idea that local similarities in the periodic nature of the black and white stripe pattern are optimal for inducing aliasing when viewed by flying insects.

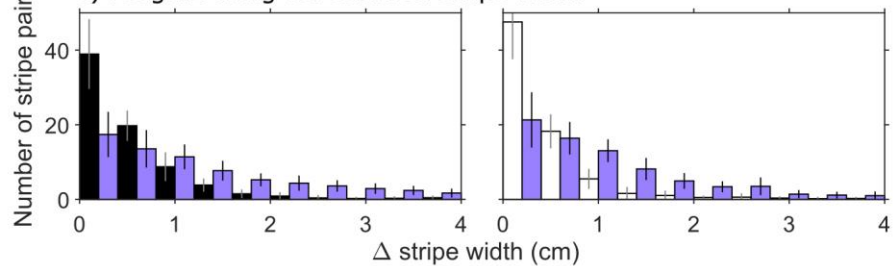
a) Measurement transect



b) Neighbouring vs. shuffled stripe angle



c) Neighbouring vs. shuffled stripe width



d) Same vs. opposite coloured stripes

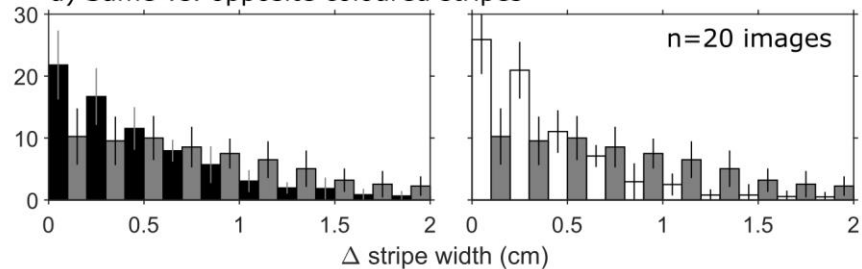


Figure 3. Analysis of neighbouring stripe angle and width from 20 images of different plains zebras. a) Illustration of transect method. Red transect roughly bisects the major parts of the animal. Where this encounters stripes, the width and angle are measured (light blue = black stripe width, purple = white stripe width). b) Distribution of difference in black (left) and white (right) stripe angle between neighbouring stripes (black and white bars respectively) and randomly shuffled stripes from the same data (blue bars). Mann-Whitney comparison within each image of neighbouring vs. shuffled stripe difference: black angle $p < 0.0001$; white angle $p < 0.0001$; $n = 52-94$ stripes in each of 20 images. c) As for (b) but analysing differences in stripe width. Black vs. shuffled thickness $p < 0.002$; white vs. shuffled thickness $p < 0.01$. d) Difference in stripe width between neighbouring stripes of the same colour (black left and white right) compared with neighbouring stripes of the opposite colour (grey bars). Error bars represent standard deviation across all 20 sample images.

A second parameter to consider for the effectiveness of aliasing as a mechanism for repelling flies is the resolving power of the horsefly visual system. As a minimum, the angular size of the zebra's black and white stripes must be the same or larger than the ommatidial acceptance angle of the fly's compound eye to be observed in high contrast. If we assume an interommatidial angle of approximately 1 degree and an average zebra stripe width of approximately 35mm (Caro et al., 2014; How and Zanker, 2014), then aliasing can only occur within fly-zebra distances of approximately 2m. It is also known that motion detection in flying insect optomotor systems tends to operate with some spatial pooling of information (Chakravarthi et al., 2018), and so we can expect a lower functional resolution that would further reduce effective range. These observations suggest that for aliasing to explain the fly repelling properties of zebras, we need to be looking for effects on fly behaviour at distances of <2m and likely <1m from the zebra body. Figure 4 shows that *Haematotopa pluvialis* failed to significantly slow their approaches to patterned horse coats compared to grey coats between 0.1 and 0.6m from the target horse. This is slightly closer than we predicted but in the correct range of distances (How et al., 2020).

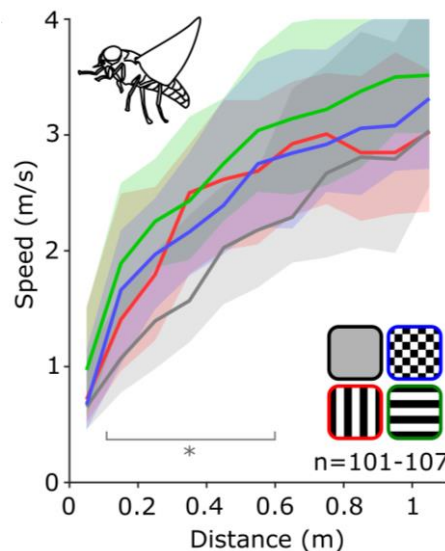


Figure 4. Approach speed of horseflies around horses wearing four different rug patterns (insert). Redrawn from How et al. 2020.

Disruption of targeting system

A third possibility is that the stripe pattern of zebras may challenge the visual system involved in host targeting. To locate and home in on a bloodmeal host, a biting fly must have a system that lets the animal detect and orient towards its target. This system would not rely directly on optic flow for its function, but on the retinal location of a set of (likely innately defined) image parameters associated with host appearance. By maintaining these image parameters in the anterior part of the visual field, the animal will home in on its host while using optic flow in parallel to control its flight kinematics. The use of this kind of targeting behaviour is widespread in insects. For example, pollinating insects use a range of colour and contrast cues to home in on flowers (Goulson, 2000; Amaya-Márquez, 2009; Chittka et al., 1999; Goulson, 1999), some butterflies use leaf shape, colour and polarization to locate plant hosts for oviposition (Rausher, 1978, 1985; Courtney, 1983; Gamberale-Stille et al., 2019; Kelber et al., 2001; Blake et al., 2019), dragonflies, hoverflies and robber flies are primed to detect and intercept small, dark, moving targets viewed against the sky (Nordström and O'Carroll, 2006; O'Carroll, 1993; Wardill et al., 2017), and several flying

insect species use the polarization of light reflected from bodies of water to locate appropriate egg laying sites (Schwind, 1991; Kriska et al., 1998). There is ample evidence from trapping studies and experimental observations that horseflies use particular visual cues to home in on mammal hosts for blood meals. Common themes that emerge are that dark and glossy solid-coloured objects are most attractive to a range of tabanid species (Horváth et al., 2019; Horváth et al., 2020; Caro et al., 2019). Additionally, linearly polarized reflections or directly filtered light (using polaroid filter) may contribute as an attractive cue (see below) (Meglič et al., 2019; Egri et al., 2012a).

Let us consider what might happen to the targeting cues used by a horsefly as it approaches a potential zebra host. From a distance, the host will appear as a solid grey object with a continuous region of polarization reflected from its dorsal surface. This is because the fine-scale stripe pattern will fall below the resolving power of the horsefly's compound eyes (How and Zanker, 2014). Then, as the horsefly approaches within 2m or less (How et al., 2020) and begins to resolve the stripe pattern, the target will transition from being homogenous grey and polarized to a highly contrasting pattern of black/white polarized/unpolarized stripes. This visual transition may be sufficient to disrupt targeting, causing the horsefly to abort its approach.

Polarization

The possibility that the polarization of light may contribute to the targeting mechanism of biting flies has been investigated in some detail. Briefly, polarization refers to the distribution of electric vectors of photons making up a beam of light (Foster et al., 2018). When sunlight or skylight reflects from the dorsal surface of glossy animal pelts, the specular reflections can be polarized by >50% with a predominantly horizontal angle of polarization (AoP) (Horváth et al., 2017). This effect is strongest when scattered light from the animal's hide pigment is low (i.e., when the pelt is dark in shade) (Horváth et al., 2010). Similarly, light reflected from bodies of water or damp areas of ground can also be strongly polarized and this cue is used by a range of insect species to locate suitable habitat or oviposition sites (Kriska et al., 1998; Schwind, 1991; Schneider and Langer, 1969). To be able to detect these polarization cues from the environment, insects have evolved dichroic photoreceptors (Stockhammer, 1956; Israelachvili and Wilson, 1976) that are sensitive to the polarization of light within a given spectral range. In many insects, this type of polarization-sensitive cell is confined to the celestially-directed dorsal-rim-area, which mediates the polarization sky compass sense (Wehner, 1976). In some biting flies (including horseflies) and water-seeking insects, polarization-sensitivity is also distributed across the ventral and forward-facing parts of the eye, allowing the detection of contrasts in polarization from smaller parts of the below- and near-horizon visual scene (Schwind, 1983; Meglič et al., 2019; Schneider and Langer, 1969).

There are plenty of experimental data in the literature suggesting that biting insects, such as horseflies, are attracted to host-like targets using polarization cues (Egri et al., 2012a; Meglič et al., 2019; Horváth et al., 2019; Horváth et al., 2020; Horváth et al., 2017; Horváth et al., 2008). However, fully controlled manipulations of polarization in field experiments are exceptionally difficult to achieve and it must be noted that, because of this, the precise contribution of polarization for host targeting remains unclear. In all of these studies, experimentally induced polarization contrasts always occur in conjunction with intensity and/or spectral contrasts and so we cannot completely disentangle the effects of polarization from concurrent intensity or spectral variations in the scene. Typically, these experiments test the attractiveness of dark polarized targets relative to light unpolarized targets (Horváth et al., 2008; Egri et al., 2012b; Horváth et al., 2010), and so there is a clear

confound between polarization and intensity. A step closer is provided by studies comparing the effectiveness of dark glossy (and therefore polarized) targets relative to matt (Meglič et al., 2019; Egri et al., 2012b). However, as well as modifying the polarization reflections, these targets also show clear differences in reflected colour and brightness. A step closer still is the study of Egri et al. (2012a), which used host-like horsefly traps constructed from polaroid filter. When viewed orthogonally, these traps varied only in polarization, but when viewed off-axis (for example by a horsefly approaching at an oblique angle) the traps also show intensity differences depending on the orientation of the polaroid (Foster et al., 2018), and so this study cannot conclusively demonstrate the sole role of polarization in host finding. The study of Meglič et al (2019) provided good evidence that horseflies may use a combination of spectral and polarization cues to highlight host-like objects in the visual scene, outlining a plausible visual mechanism for this involving opponent mechanisms in the R7 and R8 photoreceptor cells of two stochastically distributed subtypes of ommatidia. This is currently the best working hypothesis for the involvement of polarization cues for host-finding, but even this study acknowledges the difficulty of independently controlling polarization cues in the field. Future experiments should aim to disentangle these visual cues and demonstrate the relative importance and interactions between polarization, intensity, and wavelength for attracting horseflies to bloodmeal hosts.

If we accept that biting flies can use polarization as part of a suite of host-finding cues, what effect then does zebra striping have on this? The low amount of light scattered by internal pigments in dark pelage means that the light observed in these areas tends to be dominated by polarized reflections (witness the glossy sheen of black pelts). In contrast, the light observed from white areas of pelage tends to be dominated by the unpolarized light scattered from hair pigments and supporting structures (Horváth et al., 2010; Foster et al., 2018). For zebras, therefore, the stripes will appear black and white, and simultaneously polarized and unpolarized respectively, particularly near the dorsal surface of the animal but far less so on the flank and legs (Egri et al., 2012a). Disruption of this polarization pattern could play an important role in confusing the targeting system (see previous section) in parallel with effects on intensity and wavelength. Because of the difficulty of experimentally manipulating the polarization of striped objects independent of their intensity or hue, we have yet to find clear evidence that the disruption of polarization underpins the mechanism of the anti-biting fly function of zebra stripes. Future work could aim to elicit host-finding behaviour in controlled lab conditions in which striped polarized host cues can be delivered using carefully calibrated liquid crystal display panels (see Smithers et al., 2019 for an example display system). Such attempts to-date have been hindered by the difficulty of producing enough short-wavelength radiant light from these displays and by problems eliciting host-finding behaviour in the lab. Field studies paying attention to where flies land on targets (e.g., comparing landings on the polarized dorsum and upper flank vs. unpolarized vertical flank) could also uncover the involvement of polarization in host targeting, and attention could also be paid to timing and location of landings since sun angle affects degree of polarization. Because polarization, intensity and spectral cues are rarely independent in nature it seems quite possible that these work in concert in zebra stripes to disrupt the host targeting system of approaching flies.

Assumptions about biting flies being the evolutionary driver of striping

For biting flies to be the driver of striping in equids, we need to verify some implicit ecological assumptions concerning host-parasite sympatry, microhabitat overlap, abundance of biting flies, and the nature of the diseases carried by these vectors (see Caro, 2016). We review these here.

Do zebras occupy the same geographic range as biting flies?

One of the most compelling arguments for stripes being an evolutionary response to attack by biting flies is that the geographic range overlap of striped equids corresponds to that of tabanids (Caro et al., 2014) and to a lesser extent glossinids (Caro et al., 2014; Larison et al., 2015). Specifically, the ranges of the three zebra species coincide with areas characterized by 7 or more consecutive months where temperature and humidity conditions are excellent for tabanid reproduction and with areas formerly inhabited by glossinids (Figure 5). The difficulties here are that the environmental variables are approximations of tabanid abundance as no maps of tabanid species abundance or diversity are available for Africa. Furthermore, *Stomoxys* were not examined in the above comparative studies.

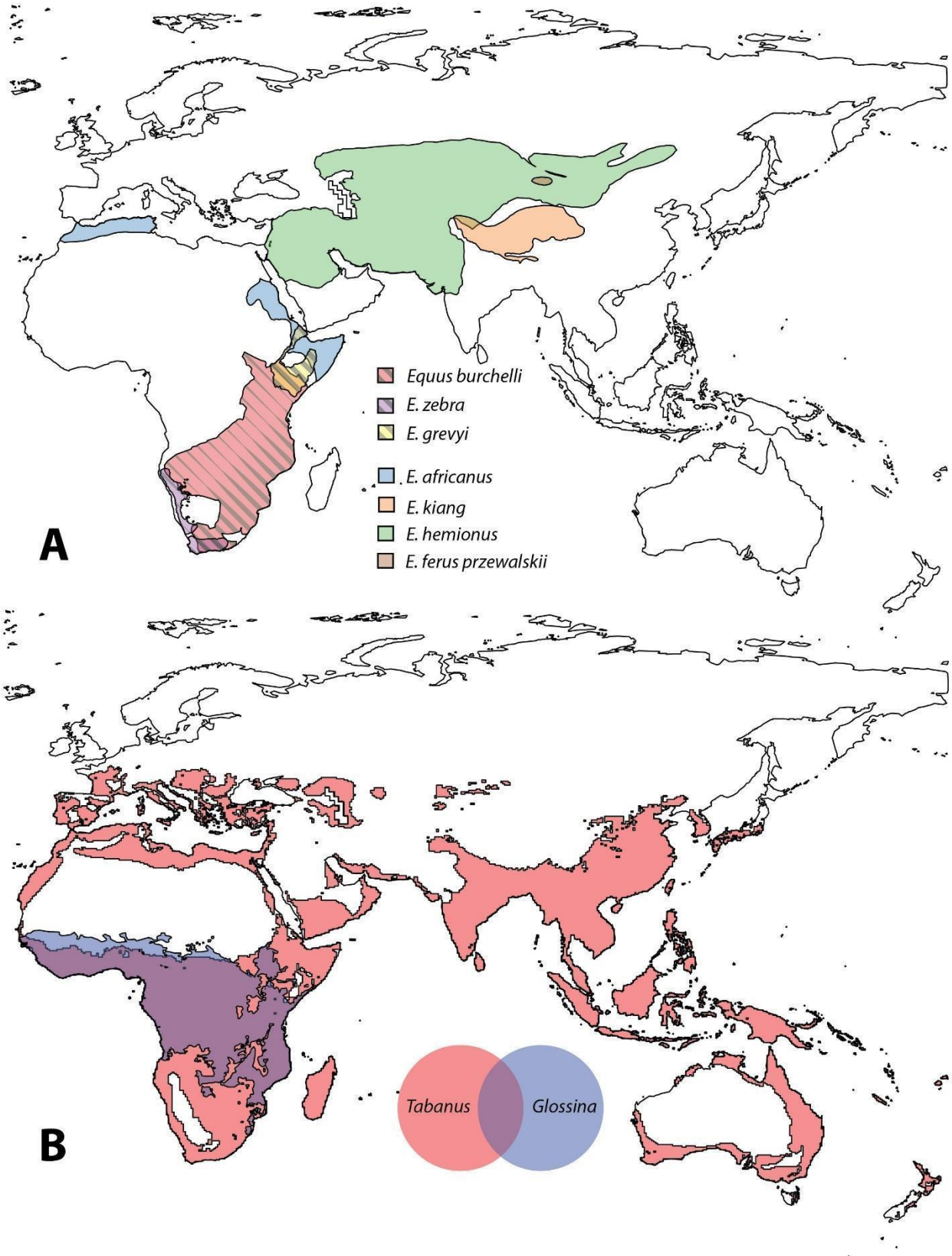


Figure 5. Distributions of equids, tabanids and glossinids. (A) Geographic distribution of 7 species of equids. (B) Map of the Old World showing distribution of tsetse flies (*Glossina*) and location of 7 consecutive months of tabanid activity (see Caro et al., 2014).

Do zebra habitat preferences correspond to those of biting flies?

The second question is whether zebra habitat preferences overlap with those of biting fly habitat preferences. Modern equids are grazers and, in line with this, the ranges of plains zebra (Table 2a), Grevy's zebra (Table 2b) and especially mountain zebra (Table 2c) currently overlap open grassland habitats. Of the 17 plains zebra studies we could find, 14 mentioned zebras using grasslands, whereas 7 mentioned woodland. Of the 6 Grevy's zebra studies, 6 mentioned grassland, 5 woodlands. Twelve out of 13 mountain zebra studies reported grassland, 1 stated woodland. Nonetheless, mountain zebra's (*Equus zebra*) and Grevy's zebra's (*Equus grevyii*) geographic ranges are now very contracted compared to the 1900s (Moehlman, 2002). A number of populations show diurnal movements between flooded grasslands in the day and surrounding woodlands at night. This suggests that zebras can escape attention of those diurnal biting flies that are restricted to woodlands.

Table 2 Habitats used by the three species of zebra

(a) Plains zebra

<u>Study Area</u>	<u>Vegetation Type</u>	<u>Movements</u>	<u>Reference</u>
Yabelo Wildlife Sanctuary, Ethiopia	Open grassland in wet season, woodland in dry season <i>Themeda triandra</i> (27.5%), <i>Cynodon dactylon</i> (20.4%), <i>Setaria verticillata</i> (13.5%)	Peak activities in early morning and late afternoon, resting peak during mid-day, time devoted to grazing peaked during dry season	(Regassa and Yirga, 2013)
Lake Nakuru NP, Kenya	Grassland on lake shore during dry season, but not in wet season		(Ogutu et al., 2012)
	Grassland, avoid woodland. Tall, low quality grass		(Mwangi and Western, 1998)
Mara Park, Kenya	Grassland, avoid savannah. Riverine habitat		(Sinclair, 1985)
Narok District, Kenya	Dwarf-shrub shrubland and grassland in wet season		(Stelfox et al., 1986)
Ranches in the southern Rift Valley, Kenya		Densities were 7x higher at night when humans and livestock were absent	(Schuette et al., 2016)
Majete Wildlife Reserve, Malawi		Waterholes visited at 9:00, 13:00 and 14:00. More time allocated to resting during dry season	(De Vos, 2020)
Etosha NP, Namibia	Wet season: grass > shrub > mopane. Dry season migratory: grass ≈ shrub > mopane.	Migratory zebras arrive at water sources at 08:38, non-migratory at 09:29; migratory zebra arrive at water sources at night, non-migratory do not	(Zidon et al., 2017)

	Dry season non-migratory: shrub > grass > mopane		
Ezemvelo Nature Reserve, S. Africa		Feeding activity is highest during afternoon	(Coetzee, 2012)
Nech Sar NP, S. Africa	More abundant on open woodland as less competition with cattle. Habitat with adequate supply of nourishment		(Abera and Tekalign, 2020)
Lake Manyara NP, Tanzania		Morning activity, afternoon activity observed if food is less abundant, night activity rarely observed	(Beekman and Prins, 1989)
Serengeti NP, Tanzania	Open grassland, woodland		(Seeber et al., 2018)
	Grassland and woodland in wet season, woodland only in dry season		(Bukombe et al., 2018)
	Woodlands in dry season, short grass plains in wet season	Grazing time higher during morning and later afternoon than midday (nighttime not included). Seasonal migration	(Seeber et al., 2019)
Lake Mburo NP, Uganda	Feed closer to mound areas of termitaria vegetation compared to adjacent savannah		(Mobæk et al., 2005)
Gonarezhou NP, Zimbabwe	Higher proportion of grassland patches		(Gandiwa, 2014)
	Woody habitat in dry season		(Traill, 2003)
Zambezi NP, Zimbabwe	Mixed and grassland, avoided teak		(Mandinyenya et al., 2020)

(b) Grevy's zebra

Study Area	Vegetation Type	Movement	Reference
Alledoghi Wildlife Reserve, Ethiopia	Grassland and shrub/bush land		(Mesfin and Berhan, 2016; Kebede et al., 2012)
Isiolo District, Kenya	Grassland	Drink at night in the pastoralist area	(Williams, 1998)
Laisamis and El Barta, Kenya	Grassland > bushland > shrubland		(Low et al., 2008)
Lewa Wildlife Conservancy, Kenya	High grass biomass		(Mwololo, 2000)
Mpala Ranch and El Karama of	Lactating females and bachelors use green, short		(Sundaresan et al., 2008)

central Laikipia, Kenya	grass and medium-dense bush more		
Samburu-Buffalo Springs Game Reserve, Kenya	Woodland and bushland		(Becker and Ginsberg, 1990)

(c) Mountain zebra

Study Area	Vegetation Type	Movement	Reference
A collection of 8 reserves, S. Africa	High grass abundance		(Lea et al., 2016)
Bakkrans Nature Reserve, S. Africa	High grass coverage and palatable grass	Waterhole used peaking at 19:00 and 20:00	(Oliver, 2019)
Baviaanskloof Nature Reserve, S. Africa	Kouga grassy Fynbos <i>Tristachya leucothrix</i> (39.4%), <i>Themeda triandra</i> (27.6%)		(Weel et al., 2015)
Bontebok NP, S. Africa	Drainage Line and Kraal Lawn vegetation		(Watson et al., 2011)
Daan Viljoen Game Reserve, Namibia		Peak grazing activity shortly after first light for 2-3 hours, and then intensified again at 15:00 until last light	(Joubert, 1972)
De Hoop Natural Reserve, S. Africa	Fynbos habitat		(Smith et al., 2011)
Gamka Mountain Nature Reserve, S. Africa	<i>Themeda triandra</i> - <i>Merxmullera stricta</i> and <i>Protea nitida</i> - <i>Themeda triandra</i> habitats		(Watson et al., 2005)
Kammanassie Nature Reserve, S. Africa	Arid Restioid Fynbos and Waboomveld habitat		(Watson and Chadwick, 2007)
Mountain Zebra NP, S. Africa	Grassland, shrubland and dwarf shrubland with high grass biomass		(Winkler and Owen-Smith, 1995)
		Seasonal migration from plateau to hill slopes in winter due to nutrient availability	(Novellie et al., 1988)
	Rocky and degraded plateau grassland, degraded dwarf shrubland	Feeding height 40-80 mm above ground	(Grobler, 1983)
	Grassland (particularly in wet season), mountain slopes and ravines (dry season)		(Skinner and Chimimba, 2005)
	High abundance of palatable grass		(Novellie and Winkle, 1993; Novellie, 1994)

	Short grasses and dwarf shrubs		(Penzhorn and Novellie, 1991)
Namibia	Plains habitat, and prefer hills and mountains		(Gosling et al., 2018)

Turning to biting flies living in Africa, it is well known that both tabanids and glossinids have uneven distributions: populations achieving very high localized densities in some areas but not others (Glasgow, 1946, 1963; Cecilia et al., 2021). We found studies documenting 8 genera of tabanids in Africa occupying habitats ranging from montane to mangrove at sea level. (Table 3a). Specifically, studies of *Ancala* species listed riverine (3 studies), woodland-savannah (1) and mangrove (1); *Atylolits* woodland-savannah (2), grassland (1); and *Chrysops* riverine (1), forest (4), woodland-savannah (1), grassland (5) and montane (5). *Haematotopa* species were found in forest (5), woodland-savannah (4), mangrove (3) and montane (3) areas; and *Tabanus* in riverine (3), forest (8), woodland-savannah (5), grassland (3), mangrove (7) and montane (5). Tabanids lay their eggs in moist mud close to standing bodies of water (Cameron, 1934; Mullens, 2019) which are found in all these areas. Tabanids' wide habitat tolerance of both grassland and woodland resembles that of plains and Grevy's zebras but are less characteristic of the current areas inhabited by mountain zebras.

Glossinids fall into three major subgenera: *palpalis* principally occupying riverine habitats; *fusca*, living in forested habitats; and *morsitans* found in savannah habitats (Jordan, 1993; Moore and Messina, 2010). We found several studies describing habitat preferences of 11 species, 15 of which reported riverine habitat, 12 forest and 11 woodland-savannah (Table 3b). Glossinids larviposit in shady dry or moist areas, must rest in habitats with trees or thickets and not in purely grassland areas. At those times when zebras are on floodplains, they can generally avoid the attention of these parasites.

There are 13 species of *Stomoxys* in Africa (Dsouli-Aymes et al., 2011) of which we could find habitat preferences of only six. Studies reported woodland-savannah (6) and grassland (3) occupancy (Table 3c). They lay eggs on fresh organic material or on faeces and are not constrained to be near water (Crosskey, 1993).

In summary, the spatial distribution of these groups overlap with those of zebras and zebras will encounter them wherever they travel, although zebra populations that restrict their diurnal movements to grassland areas can avoid glossinids.

Table 3. Habitats in Africa used by (a) tabanids, (b) glossinids, and (c) *Stomoxys*.

(a) Tabanids

Species	Habitat	Country / Area	Reference
<i>Ancala</i>			
<i>A. africana</i>	Riverain	Sudan	(Lewis, 1953)
	Sudan savannah	Nigeria	(Crosskey and Crosskey, 1955)
	Sahel savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>A. fasciata</i>	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
	Riverain	Sudan	(Lewis, 1953)
<i>A. latipes</i>	Riverain	Sudan	(Lewis, 1953)
<i>Atylotus</i>			
<i>A. agrestis</i>	Marshy grassland	Cameroon	(Mamoudou et al., 2016)
	Sahel savannah	Nigeria	(Crosskey and Crosskey, 1955)

<i>A. fuscipes</i>	Sudan savannah	Nigeria	(Crosskey and Crosskey, 1955)
Chrysops			
<i>C. beameri</i>	Bog	Kenya	(Drees, 1982)
<i>C. brucei</i>	Riverain	Sudan	(Lewis, 1953)
<i>C. dimidiata</i>	High forest	Nigeria	(Crosskey and Crosskey, 1955)
<i>C. distinctipennis</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>C. fuliginosus</i>	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
<i>C. funebris</i>	Dense forest	Sudan	(Lewis, 1953)
<i>C. geminatus</i>	Bog	Kenya	(Drees, 1982)
<i>C. longicornis</i>	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
<i>C. macquarti</i>	Bog	Kenya	(Drees, 1982)
<i>C. silacea</i>	Dense forest	Sudan	(Lewis, 1953)
	High forest	Nigeria	(Crosskey and Crosskey, 1955)
	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
<i>C. univitattus</i>	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
<i>C. vittatus</i>	Bog	Kenya	(Drees, 1982)
Haematopota			
<i>H. rubens</i>	Thicket	Rhodesian	(Phelps and Vale, 1976)
<i>H. angustifrons</i>	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
<i>H. decora</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
<i>H. exiguicornatum</i>	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
<i>H. griseicoxa</i>	Dense forest	Sudan	(Lewis, 1953)
<i>H. heptagramma</i>	Montane	Nigeria	(Crosskey and Crosskey, 1955)
<i>H. hirta</i>	High mountains	Sudan	(Lewis, 1953)
<i>H. laccessens</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>H. maculosifacies</i>	Thicket	Rhodesian	(Phelps and Vale, 1976)
<i>H. nefanda</i>	Dense forest	Sudan	(Lewis, 1953)
<i>H. nocens</i>	Thicket	Rhodesian	(Phelps and Vale, 1976)
<i>H. pallidipennis</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>H. pertinens</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>H. ugandae</i>	High mountains	Sudan	(Lewis, 1953)
Hippocentrum			
<i>H. concisum</i>	Montane	Nigeria	(Crosskey and Crosskey, 1955)
<i>H. strigipenne</i>	Dense forest	Sudan	(Lewis, 1953)

<i>H. vesicolor</i>	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
Pangonia			
<i>P. zonata</i>	The Red Sea Hills	Sudan	(Lewis, 1953)
Tabanocella			
<i>T. perpulcra</i>	Dense forest	Sudan	(Lewis, 1953)
Tabanus			
<i>T. besti</i>	Dense forest	Sudan	(Lewis, 1953)
	High forest	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. biguttatus</i>	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
	Riverain	Sudan	(Lewis, 1953)
<i>T. brumpti</i>	Dense forest	Sudan	(Lewis, 1953)
<i>T. camelarius</i>	The Red Sea Hills	Sudan	(Lewis, 1953)
<i>T. conformis</i>	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. donaldsoni</i>	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. gratus</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. insignis</i>	High mountains	Sudan	(Lewis, 1953)
<i>T. kingi</i>	The Red Sea Hills	Sudan	(Lewis, 1953)
<i>T. leucostomus</i>	The Red Sea Hills	Sudan	(Lewis, 1953)
<i>T. liventipes</i>	Thicket	Rhodesian	(Phelps and Vale, 1976)
<i>T. mordax</i>	The Red Sea Hills	Sudan	(Lewis, 1953)
<i>T. nigripes</i>	Bog	Kenya	(Drees, 1982)
<i>T. nyasae</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. obscurefumatus</i>	High forest	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. obscurehirtus</i>	High forest	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. par</i>	Marshy grassland	Cameroon	(Mamoudou et al., 2016)
	Riverain	Sudan	(Lewis, 1953)
	Sahel savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. ruficrus</i>	Dense forest	Sudan	(Lewis, 1953)
<i>T. secedens</i>	High forest	Nigeria	(Crosskey and Crosskey, 1955)
	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. seledens</i>	Mangrove and freshwater swamp forest	Nigeria	(Itina et al., 2013)
<i>T. severini</i>	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. subangustus</i>	Guinea savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. taeniola</i>	Mangrove	Nigeria	(Crosskey and Crosskey, 1955)
	Marshy grassland	Cameroon	(Mamoudou et al., 2016)
	Sahel savannah	Nigeria	(Crosskey and Crosskey, 1955)
<i>T. thoracinus</i>	Riverain	Sudan	(Lewis, 1953)

(b) Glossinids

Species	Habitat	Country / Area	Reference
Glossina			
<i>G. austeni</i>	Indigenous forest edge	South Africa	(Esterhuizen et al., 2005)
<i>G. brevipalpis</i>	Forest associated with water courses	East Africa	(Vreysen et al., 2013)
	Indigenous forest and grassland	South Africa	(Esterhuizen et al., 2005)
<i>G. caliginea</i>	Riverine and lacustrine	Gabon	(Essono et al., 2015)
<i>G. fusca</i>	Dense forest	Sub-Saharan	(Syed and Guerin, 2004)
<i>G. fusca congolensis</i>	Riverine and lacustrine	Gabon	(Essono et al., 2015)
<i>G. fuscipes</i>	Riverine	Ethiopia	(Desta et al., 2013)
<i>G. fuscipes fuscipes</i>	Riverine	Uganda	(Albert et al., 2015)
	Riverine and lacustrine	Gabon	(Essono et al., 2015)
<i>G. longipennis</i>	Acacia woodland	Kenya	(Brightwell et al., 1992)
<i>G. morsitans</i>	Miombo	Tanganyika	(Potts, 1937)
	Riverine	Ethiopia	(Desta et al., 2013)
	Savannah	Sub-Saharan	(Syed and Guerin, 2004)
	Woodland	Zimbabwe	(Williams et al., 1994)
<i>G. morsitans morsitans</i>	Dense woodland	Zambia	(Alderton et al., 2018)
	Miombo and Munga	Zambia	(Van den Bossche and De Deken, 2002)
	Vicinity of escarpment	Zimbabwe	(Shereni et al., 2016)
<i>G. morsitans spp.</i>	Savannah woodlands	Eastern and southern Africa	(Vreysen et al., 2013)
<i>G. morsitans submorsitans</i>	Dry canopied woodland	The Gambia	(Rawlings et al., 1993)
	Game reserves and forests	Togo	(Hendrickx et al., 1999)
	Valley	Cameroon	(Mamoudou et al., 2008)
<i>G. pallicera newsteadii</i>	Riverine and lacustrine	Gabon	(Essono et al., 2015)
<i>G. pallidipes</i>	Closed riverine and thickets	Kenya	(Brightwell et al., 1992)
	Riverine	Ethiopia	(Desta et al., 2013)
	Savannah woodlands	Eastern and southern Africa	(Vreysen et al., 2013)
	Vicinity of escarpment	Zimbabwe	(Shereni et al., 2016)
	Woodland	Zimbabwe	(Williams et al., 1994)
<i>G. palpalis</i>	Lowland rain forest	West Africa	(Vreysen et al., 2013)
	Riverine	West Africa	(Rogers and Randolph, 1986)
	Riverine gallery forest	Sub-Saharan	(Syed and Guerin, 2004)
<i>G. palpalis gambiensis</i>	Evergreen forest, woodland and riverine	The Gambia	(Rawlings et al., 1993)
<i>G. palpalis palpalis</i>	Riverine and lacustrine	Gabon	(Essono et al., 2015)
<i>G. tachinoides</i>	Game reserves and forests	Togo	(Hendrickx et al., 1999)
	Riverine	Ethiopia	(Desta et al., 2013)
	Riverine	West Africa	(Rogers and Randolph, 1986)
	Val(ley	Cameroon	(Mamoudou et al., 2008)

(c) *Stomoxys*

Species	Habitat	Country / Area	Reference
<i>Stomoxys</i>			
<i>S. calcitrans</i>	Grassland	Uganda	(Harley, 1965)
	Mid-land agro-climate habitat	Ethiopia	(Dawitt et al., 2012)
	Open biotopes of secondary forest, savannah and villages	Gabon	(Essono et al., 2015)
	Pens and corridors surrounded by vegetation, holding ponds and manure run off	South Africa	(Evert, 2014)
<i>S. inornatus</i>	Open biotopes of secondary forest, savannah and villages	Gabon	(Essono et al., 2015)
<i>S. niger bilineatus</i>	Open biotopes of secondary forest, savannah and villages	Gabon	(Essono et al., 2015)
<i>S. niger niger</i>	Open biotopes of secondary forest, savannah and villages	Gabon	(Essono et al., 2015)
<i>S. nigra</i>	Grassland	Uganda	(Harley, 1965)
<i>S. omega</i>	Grassland	Uganda	(Harley, 1965)
<i>S. omega omega</i>	Open biotopes of secondary forest, savannah and villages	Gabon	(Essono et al., 2015)
<i>S. transvittatus</i>	Open biotopes of secondary forest, savannah and villages	Gabon	(Essono et al., 2015)

Biting fly activity

All three dipteran groups favour warm humid conditions (Table 4) and some prefer moist closed environments (Foil and Hogsette, 1994). These conditions are characteristic of some areas of zebras' range and zebras will encounter them when they move to woodlands in the wet season to avoid waterlogged floodplains. In the dry season, however, zebras can avoid such areas. Some populations of mountain zebras are found in dry desert habitats of Namibia and colder parts of southern Africa where these biting flies are present but less prevalent. Nonetheless, it must be acknowledged that local populations, at least of tabanids, vary annually according to variations in temperature and precipitation (Mikuška et al., 2012).

Table 4. Abiotic factors affecting the abundance of (a) tabanids, (b) glossinids, and (c) *Stomoxys* in different African countries.

(a) Tabanids

Country or Area	Humidity %	Temperature °C	Hours of Day	Other	Reference
Cameroon			06:00-18:00		(Mamoudou et al., 2016)
Kenya	Drought or long periods of abundant rains can affect the abundance				(Denlinger, 1980)

Nigeria		Optimal reproduction 22.8-24.1			(Ahmed et al., 2005)
Nigeria		27-32		Wet season preferred over dry season	(Itina et al., 2013)
Nigeria			Peak biting period 09:00-10:00 and 15:00-16:00		(Iboh et al., 2012)
Rhodesian		Mean 18-32		Attraction to CO ₂	(Phelps and Vale, 1976)
Tanzania	More active during dry sunny weather, less on cloudy days with strong monsoon winds and rainfall				(Wiesenhütter, 1975)
Uganda			Peak 11:00-14:00		(Harley, 1965)

(b) Glossinids

Country or Area	Humidity %	Temperature °C	Hours of Day	Other	Reference
Africa (south)		Maximum temperature 27.0–29.2			(Esterhuizen et al., 2005)
Africa Sub Saharan			Daytime active	Take cover under the bush <i>Lantana camara</i>	(Syed and Guerin, 2004)
Africa, central sub-Saharan	Humid				(Madsen et al., 2013)
Gabon			<i>G. p. palpalis</i> 11:00-16:00, <i>G. tabaniformis</i> at beginning and end of day		(Essono et al., 2015)
Kenya	Positive correlation	Positive correlation		Positive correlation with abundance of hosts on the plains	(Brightwell et al., 1992)
Kenya		Index of clustering negative correlation with minimum temperature for <i>G. longipennis</i> , maximum temperature for <i>G. pallidipes</i>			(Odulaja et al., 2001)
Sudan		Positive correlation			(Lukaw et al., 2014)

Uganda	Positive correlation	Positive correlation			(Albert et al., 2015)
West Africa	High			Annual rainfall 900 - 2200 mm Only for <i>G. palpalis</i>	(Rogers and Randolph, 1986)

(c) *Stomoxys*

Country or Area	Humidity %	Temperature °C	Hours of Day	Other	Reference
Africa, La Réunion Island		20-25 for immature survival			(Gilles et al., 2005)
Cameroon		Positive correlation	08:00-10:00 14:00-16:00		(Lendzele et al., 2019)
Ethiopia	Regular rains				(Dawitt et al., 2012)
Mauritius	Wet	Warm	08:00-14:30	Sugarcane cropping season	(Kunz and Monty, 1976)
Uganda			Morning, late evening		(Harley, 1965)

Are biting flies a prolonged annoyance?

Tabanids in Africa are active for a substantial portion of the year, for an average of 285 days based on 11 studies (Table 5a), far greater than tabanids in temperate regions ($X=103$ days, $N=21$ studies) or even the New World tropics ($X=153$ days, $N=3$ studies). In some countries such as Uganda, they are active year-round. Glossinids and *Stomoxys* are present in African countries throughout the year (Tables 5b and c). These diptera therefore exert a constant threat to zebras in areas where they are sympatric.

Table 5. Period that (a) tabanids, (b) glossinids, and (c) *Stomoxys* are active in different countries.

(a) Tabanids.

Country or Area	Date of Emergence	Species	Season Length (Day)	Reference
African Countries				
Nigeria	April (wet season)	<i>Chrysops silacea</i> , <i>C. univittatus</i> , <i>Tabanus seledens</i> , <i>C. longicornis</i> , <i>Haematopota exiguicornatum</i> and 6 others.	180	(Itina et al., 2013)
Nigeria	Study was carried out from September.	<i>Chrysops dimidiata</i> (69.7%) and <i>C. silacea</i> (30.3%).	180, when study ended in February. Peak in September	(Iboh et al., 2012)
Nigeria	Southern: all year round	89 species in total.	-	(Crosskey and Crosskey, 1955)

	Northern: wet seasons only			
Nigeria	Wet (85.1%) Dry (14.9%) Some species all year round	<i>Tabanus biguttatus</i> , <i>T. albipalpis</i> , <i>T. pertinens</i> and 12 others.	Wet season, April ~ October = 214	(Ahmed et al., 2005)
Sudan	All year round	Did not specify species.	365	(Lewis, 1953)
Sudan	July (rainy season)	Did not specify species.	90	(Lewis, 1953)
Sudan, East	All year round, 52.29% in wet season	Did not specify species.	365	(Crooft et al., 2017)
Tanzania	All year round	<i>Tabanus fraternus</i> , <i>T. taeniolar</i> , <i>T. gratus</i> , <i>T. biguttatus</i> , <i>Haematopota decora</i> and 7 others.	365	(Wiesenhütter, 1975)
Tanzania	September	<i>Chrysops bicolor</i>	300	(Raybould, 1967)
Uganda	All year round	<i>Tabanidae</i> spp.	365	(Neave, 1912)
Uganda	All year round	<i>Tabanus taeniola</i> , <i>T. par</i> , <i>Ancala africana</i> and 13 others.	365, peak in May-August and November-December	(Harley, 1965)
Zambia	All year round	<i>Tabanus taeniola</i> peak in November, <i>T. conformis</i> peak in October, <i>Atylotus agrestis</i> peak in April, <i>Haematopota pertinens</i> in January and 25 others.	365	(Clarke, 1968)
Zimbabwe	24 th December	<i>Haematopota nocens</i> , <i>Tabanus unilineatus</i> , <i>T. copemani</i> , <i>Philoliche silverlocki</i> , <i>H. fasciatapex</i> and 16 others.	165	(Phelps and Holloway, 1990)
Non-African, Tropical Countries				
Brazil	7 th July	<i>Tabanus importunus</i> (56%), <i>T. occidentalis</i> (8.2%), <i>T. claripennis</i> (8.1%), and <i>Lepiselaga crassipes</i> (7.7%) and 17 others.	100	(Barros, 2001)
Brazil	September	Spring peak: <i>Lepiselaga albitarsis</i> and <i>Tabanus triangulum</i> ; Spring and Summer peak: <i>Poeciloderas quadripunctatus</i> ; and 26 others.	210	(Krüger and Krolow, 2015)
Panama	Early May	<i>Tabanus lineola</i> , <i>T. maya</i> , <i>T. angustivilla</i> , <i>Dichelacera analis</i> and 31 others.	150	(Fairchild, 1942)
Non-African, Temperate Countries				

Bulgaria	15 th May	<i>Tabanus quatuornotatus</i> , <i>T. tergestinus</i> and 21 others.	120, peak in early June to July	(Ganeva and Kalmushka, 2019)
Canada	29 th June	<i>Tabanus affinis</i> , <i>T. zonalis</i> , <i>T. metabola</i> , <i>Chrysops furcate</i> , <i>T. zonalis</i> and 11 others.	51	(Miller, 1951)
Canada, Manitoba	15 th June	Did not specify species.	90	(McElligott and Galloway, 1991)
Canada, Manitoba	24 th May	Earliest: <i>Hybomitra metabola</i> and <i>H. nuda</i> Late June: <i>H. lasiophthalma</i> and <i>H. frontalis</i> <i>H. epistates</i> , <i>H. typhus</i> , <i>Tabanus similis</i> and the <i>Chrysops</i> species appear in large numbers.	67	(Hanec and Bracken, 1964)
Canada, Ontario	21 st May	<i>Tabanus trepidus</i> , <i>T. epistates</i> , <i>Chrysops vittata</i> , <i>C. montana</i> , <i>C. wiedemanni</i> and 24 other species.	82	(Davies, 1959)
France	17 th May	<i>Haematopota italica</i> (61%), <i>Tabanus glaucopis</i> (11%), <i>T. nemoralis</i> (8%), <i>T. quatuornotatus</i> (4%), <i>T. exclusus</i> (4%) and <i>T. bromius</i> (3%) and 13 others.	120, peak in late May and late August	(Azza et al., 2020)
Hungary	June	<i>Haematopota pluvialis</i> , <i>Tabanus tergestinus</i> , <i>T. bromius</i> , <i>T. maculicornis</i> , <i>T. bovinus</i> , <i>Atylotus loewianus</i> and 11 others.	90	(Herczeg et al., 2014)
Italy	June	<i>Haematopota italica</i> (36.9%), <i>Atylotus loewianus</i> (12.7%), <i>Tabanus lunatus</i> (9.1%), <i>T. bromius</i> (7.6%), <i>T. marianii</i> (5.7%) and 34 others.	120	(De Liberato et al., 2019)
Japan, Hokkaido	5 th June	<i>Haematopota tristis</i> , <i>Chrysops suavis</i> , <i>Tabanus sapporoensis</i> , <i>T. iyoensis</i> , <i>T. rufidens</i> and 12 others.	98	(Inaoka, 1975)
New York City	Early June	<i>Tabanus lasiophthalmus</i> , <i>T. quinquevittatus</i> , and <i>T. sulcifrons</i> in the order of their seasonal occurrence (<i>did not state the total number of species</i>)	90	(Tashiro and Schwardt, 1949)
North Norway	20 th June	<i>Chrysops nigripes</i> , <i>C. relictus</i> , <i>Hybomitra aterrima</i> , <i>H. kaurii</i> , <i>H. montana</i> and <i>Haematopota pluvialis</i> and 12 others.	55	(Bergersen, 2004)
Pyrenees Mountains	Early June	<i>Philipomyia aprica</i> , <i>Tabanus bromius</i> , <i>Hybomitra auripila</i> , <i>T.</i>	90	(Baldacchino et al., 2014a)

(France, Spain)		<i>glaucopis</i> , <i>H. montana</i> and 14 others.		
Pyrenees, France	July	<i>Tabanus bromiu</i> , <i>Hybomitra montana</i> , <i>H. auripila</i> , <i>H. caucasica</i> , <i>T. glaucopis</i> and 10 others.	60	(Baldacchino et al., 2014b)
Republic of Korea	15 th June	<i>Chrysops mlokosiewiczii</i> (90.9%), <i>Haematopota koryoensis</i> (4.8%), <i>C. suavis</i> (1.0%) and 17 others.	60	(Suh et al., 2015)
Turkey, Western Anatolia	7 th May	<i>Dasyrhamphis umbrinus</i> , <i>Haematopota subcylindrica</i> , <i>Philipomyia aprica</i> , <i>Tabanus bifarius</i> , <i>T. bromius</i> and 47 others.	130	(Altunsoy and Kılıç, 2012)
UK	21 st May	Did not specify species.	140	(Ball, 1984)
UK	May	<i>Haematopota pluvialis</i> and 29 others.	150	(Newitt et al., 2016)
US, Alabama	Early May	<i>Tabanus importunus</i> (56%), <i>T. occidentalis</i> (8.2%), <i>T. claripennis</i> (8.1%), <i>Lepiselaga crassipes</i> and 17 others.	105	(Burnett and Hayes, 1977)
US, Florida	18 th February	<i>Tabanus atratus fulvopilosus</i> , <i>T. lineola</i> , <i>Chrysops flavidus</i> , <i>C. hinei</i> and 31 others.	135	(Jones and Anthony, 1964)
US, New Jersey	16 th May	<i>Tabanus lineola</i> , <i>Chrysops vittatus</i> , <i>Hybomitra lasiophthalma</i> , <i>T. pumilus</i> , <i>C. callidus</i> and 28 others.	135	(Thompson, 1967)
US, Oklahoma	15 th April	<i>Tabanus abactor</i> , <i>T. atratus</i> , <i>T. equalis</i> , <i>T. mularis</i> and 19 others.	185	(Wright et al., 1984)

(b) Glossinids.

Country or Area	Date of Emergence	Species	Season Length (Day)	Reference
African Countries				
Cameroon	All year round	<i>Glossina morsitans submorsitans</i>	Peak in June to August	(Mamoudou et al., 2008)
Nigeria & Bagheri	All year round	<i>G. palpalis</i>	Peak in August to October	(Rogers and Randolph, 1986)
Nigeria & Bagheri	All year round	<i>G. tachinoides</i>	Peak in April	(Rogers and Randolph, 1986)
Sudan	All year round	<i>G. fuscipes fuscipes</i>	Higher in dry season, peak in January	(Lukaw et al., 2014)

Tanzania	All year round	<i>G. morsitans morsitans</i>	Peaked in July and March	(Nnko et al., 2017)
Tanzania	All year round	<i>G. pallidipes</i>	Peaked in November and July	(Nnko et al., 2017)
Tanzania	All year round	<i>G. swynnertoni</i>	Peaked in July, then September then March	(Nnko et al., 2017)
Tanzania, Maasai steppe	All year round	<i>G. swynnertoni</i> (70.8%), <i>G. morsitans morsitans</i> (23.4%), and <i>G. pallidipes</i> (5.8%)	Peak in July	(Nnko et al., 2017)
Togo	All year round	<i>G. palpalis palpalis</i>	Peak in January	(Hendrickx et al., 1999)
Togo	All year round	<i>G. tachinoides</i>	Peak in February	(Hendrickx et al., 1999)
Zambia	All year round	<i>G. morsitans morsitans</i>	Peak in October to November	(Alderton et al., 2018)
Zambia, Miombo	All year round	<i>G. morsitans morsitans</i>	Peak in rainy season	(Van den Bossche and De Deken, 2002)
Zambia, Munga	All year round	<i>G. morsitans morsitans</i>	Peak in dry, hot season	(Van den Bossche and De Deken, 2002)

(c) Stomoxys.

Country or Area	Date of Emergence	Species	Season Length (Day)	Reference
African Countries				
Cameroon	All year round	<i>Stomoxys calcitrans</i> , <i>S. niger bilineatus</i> , <i>S. omega</i> , and <i>S. xanthomelas</i>	Peak in May	(Lendzele et al., 2019)
Ethiopia	All year round	<i>S. calcitrans</i> , <i>S. niger</i> , <i>S. sitiens</i> , <i>S. tarniatus</i> , <i>S. inornatus</i> , <i>S. ochrosoma</i>	Peak in August-September	(Dawitt et al., 2012)
Mauritius	All year round	<i>S. nigra nigra</i> , <i>S. calcitrans</i>	Peak in September-October	(Kunz and Monty, 1976)
South Africa	Late December	<i>S. calcitrans</i>	90, peak in late January-February	(Evert, 2014)
Uganda	All year round	<i>S. nigra</i> , <i>S. calcitrans</i>	Peak in May-August, Nov-Dec	(Harley, 1965)
Non-African, Tropical Countries				
Brazil	September	<i>S. calcitrans</i>	300, peak in November-December	(Rodríguez-Batista et al., 2005)
Thailand	All year round	<i>S. calcitrans</i>	Peak in rainy season	(Muenworn et al., 2010)
Thailand	All year round	<i>S. calcitrans</i>	Peak in Sep, and March-April	(Phasuk et al., 2013)
Thailand	All year round	<i>S. calcitrans</i> , <i>S. sitiens</i> , <i>S. indica</i>	80% captured during May-October	(Masmeathip et al., 2006)
Non-African, Temperate Countries				

Canada	Study was carried out from May	<i>S. calcitrans</i>	180, when study ended in October. Peak in August-September	(Lysyk, 1993)
Canada, Manitoba	May	<i>S. calcitrans</i>	150	(Khumalo and Galloway, 1996)
New Zealand	September	<i>S. calcitrans</i>	300, peak in January-May	(Heath, 2002)
Slovakia	Week 14	<i>S. calcitrans</i>	270, peak in August-September	(Semelbauer et al., 2018)
UK, England	Mid May	<i>S. calcitrans</i>	210	(Parravani et al., 2019)
USA	Did not specify	<i>S. calcitrans</i>	Peak around 13th June	(Ose and Hogsette, 2014)
USA, California	Late April	<i>S. calcitrans</i>	75	(Mullens and Meyer, 1987)
USA, Florida	November	<i>S. calcitrans</i>	240, peak in April	(Machtinger et al., 2016)
USA, Florida	November	<i>S. calcitrans</i>	180, peak in late April	(Pitzer et al., 2011)

Do biting flies carry diseases dangerous to zebras?

While only female tabanids and female glossinids require a blood meal in order to reproduce, these three groups of biting flies (tabanids, glossinids, *Stomoxys*) can carry diseases that are very dangerous to equids. Out of a total of 20 diseases carried by tabanids that we could unearth, 14 affected equids, 9 of which could be lethal. Our review shows that tabanids carry equine infectious anemia, vesicular stomatitis, trypanosomiasis (surra, nagana), tularemia, anaplasmosis, African horse sickness, anthrax and encephalitis that are dangerous or lethal to equids (see Table 6a). Of 5 diseases carried by glossinids, 4 affect equids, 3 of which could potentially be lethal: trypanosomiasis (surra, nagana) and anthrax (see Table 6b). Of the 13 mentioned for *Stomoxys*, 9 affect equids, 6 of which are lethal: equine infectious anemia, vesicular stomatitis, anthrax, trypanosomiasis (surra and nagana), and west Nile fever (see Table 6c). Clearly, these three groups of biting flies have the potential to be a severe threat to zebras depending on whether they are vectors at the time of attack.

Unfortunately, the incidence of these diseases in fly vectors are poorly documented and principally restricted to trypanosomiasis carried by glossinids (see Table 9.6 in Caro, 2016). Just as problematic, infection rates vary by location. For instance, trypanosome infection rates in *Glossina swynnertoni* vary between 0% and 16.3% across seven sites within just the Serengeti National Park (Malele et al., 2007). This is one of the most troubling gaps in our knowledge: the extent to which lethal zebra diseases are prevalent in vector populations within zebras' ranges.

Table 6. Diseases that can be transmitted to ungulates by tabanids, glossinids and *Stomoxys*. Mechanical transmission occurs when the pathogen is transferred from one host to another by an animal vector that is not infected by the pathogen but carries it on/in a certain body part e.g., mouthparts, saliva etc. In biological transmission the pathogen must infect the animal vector, after it has bitten a diseased host, and then develop or reproduce within the animal vector before being transferred to another host.

(a) Tabanids

Disease	Pathogen	Tabanid fly species (vector)	Transmission	Recipient	Infection site and virulence	References
Equine infectious anaemia (EIA)	Equine infectious anaemia virus (EIAV)	Tabanidae (in general) <i>Tabanus fuscicostatus</i> , <i>Hybomitra lasiophthalma</i> , <i>Chrysops flavidus</i>	Mechanical	Horses	Blood infection Lethal - horse can suddenly die in acute form of disease	(Krinsky, 1976; Mullens, 2019; Hawkins et al., 1976; Ganguly and Wakchaure, 2016; Foil, 1989)
Vesicular stomatitis (VS)	Vesicular stomatitis virus (VSV)	Tabanidae	Mechanical	Horses, other equids, cattle, swine, llamas - endemic to the Americas	Mucous membrane infection Lethal	(Krinsky, 1976; McCluskey and Mumford, 2000)
Hog cholera or classical swine fever (CSF)	Hog cholera/classical swine fever virus (CSFV)	Tabanidae <i>Tabanus lineola</i>	Mechanical	Pigs, wild boar	Tonsils and lymph nodes infection Lethal - mortality rate may be as high as 90%	(Krinsky, 1976; Artois et al., 2002; Foil, 1989)
Surra (trypanosomiasis)	<i>Trypanosoma evansi</i> Kinetoplastida (protist)	Tabanidae	Mechanical	Equids, camels, cattle and many others	Blood and tissue parasite/infection Lethal - often fatal	(Mullens, 2019; Desquesnes et al., 2013)
Tularemia	<i>Francisella tularensis</i> Bacterium	Tabanidae <i>Chrysops noctifer</i> <i>pertinax</i>	Mechanical	Deer, horses, goats and many others	Macrophage (white blood cell) infection Lethal - fatality rate >50% without treatment	(Mullens, 2019; Emmons et al., 1976; Sjöstedt, 2007)
Elaeophorosis	<i>Elaeophora schneideri</i> Nematode	Tabanidae	Biological	Sheep, deer, moose	Carotid artery parasite/infection Lethal	(Mullens, 2019; Worley et al., 1972)
Lumpy skin disease (LSD)	Lumpy skin disease virus (LSDV)	<i>Haematopota</i> spp.	Mechanical	Cattle - endemic to southern, central, eastern and western Africa	Skin infection Lethal - low mortality rate	(Sohier et al., 2019)

Anaplasmosis	<i>Anaplasma marginale</i> - bovine anaplasmosis <i>A. phagocytophilum</i> - equine anaplasmosis Bacteria	Horseflies <i>Tabanus fuscicostatus</i> , <i>T. sulcifrons</i> , <i>T. lineola</i> , <i>T. mularis</i> , <i>T. pallidescens</i>	Mechanical	Cattle, horses	Red blood cell infection Lethal - mortality rate 29-49% in adult cattle	(Hungerford and Smith, 1996; Aubry and Geale, 2011; Scoles et al., 2008; Leblond et al., 2005; Foil, 1989)
African horse sickness (AHS)	African horse sickness virus (AHSV)	Horseflies	Biological	Horses, donkeys, mules, zebras (highly resistant) - endemic to Sub-Saharan Africa	Lung, spleen and lymphoid tissue infection Lethal - mortality rates in excess of 90% in horses	(Radcliffe and Osofsky, 2002; Mellor and Hamblin, 2004; Cook et al., 2001)
Anthrax	<i>Bacillus anthracis</i> Bacterium	Horseflies	Mechanical	Zebras, horses	Lymphatic tissue and spleen infection Lethal - high mortality rate	(Turnbull, 2008; Radcliffe and Osofsky, 2002; Palazzo et al., 2012; Hugh-Jones and de Vos, 2002)
Nagana (trypanosomiasis)	<i>Trypanosoma congolense</i> , <i>T. vivax</i> and <i>T. brucei</i> Kinetoplastida (protist)	Tabanidae <i>Atylotus agrestis</i>	Mechanical	Equids, cattle, warthogs, antelope, African buffaloes and many others	Blood parasite/infection Lethal - mortality rate as high as 50-100% with some strains	(Desquesnes et al., 2013; Anonymous, 2009; Desquesnes and Dia, 2003)
Babesiosis	<i>Babesia</i> spp. Apicomplexa (protist)	Tabanidae	Biological	Equids, cattle and many others	Red blood cell parasite/infection Lethal - occasionally fatal in untreated animals	(Radcliffe and Osofsky, 2002; Homer et al., 2000; Rashid et al., 2009)
Equine influenza (EI)	Equine influenza virus (EIV) 2 subtypes: A/equine-1 and A/equine-2	<i>Atylotus agrestis</i>	Mechanical	Horses	Nose, throat and lung infection Lethal - low mortality rate 1-2%	(Foil, 1989; Timoney, 1996)
Lyme disease	<i>Borrelia burgdorferi</i>	<i>Hybomitra hinei</i> , <i>Tabanus pumilus</i> , <i>T.</i>	Biological	Horses and other mammals	Skin, fascia and synovial membrane	(Magnarelli et al., 1986; Divers et al., 2001)

	Bacterium	<i>quinquevittatus</i>			infection Not lethal	
Besnoitiosis	<i>Besnoitia bennetti</i> - equine besnoitiosis <i>B. besnoiti</i> - bovine besnoitiosis Protozoan	Horseflies <i>Atylotus nigromaculatus</i> , <i>Tabanus taeniola</i>	Mechanical	Horses, donkeys, cattle	Skin, mucous membrane and conjunctiva infection Lethal - low mortality rate	(Sellon and Long, 2013; Bigalke, 1981; Foil, 1989)
Bovine leukaemia	Bovine leukaemia virus (BLV)	Tabanidae <i>Tabanus fuscicostatus</i> , <i>T. nipponicus</i>	Mechanical	Cattle, sheep, goats, zebus, buffaloes	Lymphocyte (white blood cell) infection Lethal - low mortality rate 1-5%	(Foil, 1989; Schwartz and Lévy, 1994)
Trypanosomiasis	<i>Trypanosoma theileri</i> Kinetoplastida (protist)	Tabanidae	Biological	Cattle, wild mammals	Blood parasite/infection Not lethal - very low pathogenicity	(Foil, 1989; Villa et al., 2008)
Rinderpest (extinct)	Rinderpest virus (RPV) (extinct)	<i>Tabanus sp.</i> , <i>T. orientis</i>	Mechanical	Cattle, wild artiodactyls (buffaloes, wildebeest, giraffes)	Lymphatic tissue infection Lethal - high mortality rate 50-90%	(Krinsky, 1976; Dobson et al., 2011; Roeder and Taylor, 2002)
Equine encephalitis (EE)	Eastern equine encephalitis virus (EEEV) Western equine encephalitis virus (WEEV)	<i>Tabanus punctifer</i> , <i>T. nigrovittatus</i>	Unknown	Horses	Brain and cerebrospinal fluid (CNS) infection Lethal	(Krinsky, 1976; Carrera et al., 2013; Deresiewicz et al., 1997)
Tick-borne encephalitis	Tick-borne encephalitis virus (TBEV)	<i>Tabanus flavicornis</i>	Unknown	Horses, goats, cattle, sheep, deer, swine and others	Brain and cerebrospinal fluid (CNS) infection Lethal	(Krinsky, 1976; Dumpis et al., 1999; Rushton et al., 2013)

Q fever	<i>Coxiella burnetii</i> Bacterium	<i>Tabanus staegei</i>	Unknown (likely mechanical)	Cattle, sheep, goats	Monocyte/macrophage (white blood cell) infection Not lethal - most animals asymptomatic, however, abortion rates vary 3-80%	(Krinsky, 1976; Angelakis and Raoult, 2010)
Blackleg	<i>Clostridium chauvoei</i> Bacterium	<i>Tabanus rubidus</i>	Unknown	Cattle, sheep, deer	Skeletal and cardiac muscle infection Lethal - many animals die within 36 hours after onset of clinical signs	(Krinsky, 1976; Abreu et al., 2017)
Hemorrhagic septicemia/buffalo sickness	<i>Pasteurella multocida</i> Bacterium	<i>Tabanus rubidus, T. striatus, Chrysops dispar</i>	Mechanical	Buffaloes, cattle	Blood infection Lethal - mortality rate up to 100%	(Krinsky, 1976; Shivachandra et al., 2011)
Brucellosis	<i>Brucella abortus</i> - bovine brucellosis <i>B. suis</i> - suid brucellosis <i>B. melitensis</i> - ovine/caprine brucellosis Bacteria	<i>Chrysozona italica, C. pluvialis, Sziladynus solstitialis, Tabanus bovinus, T. glaucopsis, Heptatoma pellucens, T. sudeticus</i>	Mechanical	Cattle, sheep, goats, pigs	Lymph node infection Lethal - low mortality rate, abortion common	(Krinsky, 1976; Godfroid, 2002; Neilsen and Duncan, 1990)
Listeriosis	<i>Listeria monocytogenes</i> Bacterium	Tabanidae	Mechanical	Cattle, sheep, goats	CNS and blood infection Lethal - abortion common	(Krinsky, 1976; Low and Donachie, 1997)
Swine erysipelas/diamond skin disease	<i>Erysipelothrix rhusiopathiae</i> Bacterium	<i>Chrysozona pluvialis, Tabanus bromius, Heptatoma pellucens</i>	Mechanical	Swine	Skin infection Lethal - death rate varies 0-75%	(Krinsky, 1976; Shuman and Osteen, 1956)

Leptospirosis	<i>Leptospira interrogans</i> Bacterium	<i>Tabanus bromius</i>	Mechanical	Cattle and other mammals	Liver and kidney infection Lethal - low mortality rate, abortion common	(Krinsky, 1976; Lilenbaum and Martins, 2014)
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(b) Glossinids

Disease	Pathogen	Glossinid fly species (vector)	Transmission	Recipient	Infection site and virulence	References
Nagana (trypanosomiasis)	<i>Trypanosoma congolense</i> , <i>T. vivax</i> and <i>T. brucei</i> Kinetoplastida (protist)	Tsetse flies <i>Glossina morsitans morsitans</i>	Biological	Equids, cattle, warthogs, antelope, African buffaloes and many others	Blood parasite/infection Lethal - mortality rate as high as 50-100% with some strains	(Anonymous, 2009; Desquesnes et al., 2013; Roberts et al., 1989)
Surra (trypanosomiasis)	<i>Trypanosoma evansi</i> Kinetoplastida (protist)	Tsetse flies	Biological	Equids, camels, cattle and many others	Blood and tissue parasite/infection Lethal - often fatal	(Desquesnes et al., 2013; Mullens, 2019)
Besnoitiosis	<i>Besnoitia bennetti</i> - equine besnoitiosis <i>B. besnoiti</i> - bovine besnoitiosis Protozoan	Tsetse flies	Mechanical	Horses, donkeys, cattle	Skin, mucous membrane and conjunctiva infection Lethal - low mortality rate	(Sellon and Long, 2013; Bigalke, 1981)
Anthrax	<i>Bacillus anthracis</i> Bacterium	Tsetse flies	Mechanical	Zebras, horses	Lymphatic tissue and spleen infection Lethal - high mortality rate	(Radcliffe and Osofsky, 2002; Turnbull, 2008; Palazzo et al., 2012; Hugh-Jones and de Vos, 2002; Blackburn et al., 2014)
Heartwater	<i>Ehrlichia ruminantium</i> Bacterium	Tsetse flies	Mechanical	Cows, sheep, goats (ruminants)	Endothelial cell infection Lethal - commonly fatal within a week	(Hornok et al., 2016; Peter et al., 2002; Clifford, 2006)

(c) Stomoxys

Disease	Pathogen	Stomoxys fly species (vector)	Transmission	Recipient	Infection site and virulence	References
Equine infectious anaemia (EIA)	Equine infectious anaemia virus (EIAV)	<i>S. calcitrans</i> <i>S. niger</i> <i>S. sitiens</i> <i>S. indicus</i>	Mechanical	Horses	Blood infection Lethal - horse can suddenly die in acute form of disease	(Baldacchino et al., 2013; Ganguly and Wakchaure, 2016)
Lumpy skin disease (LSD)	Lumpy skin disease virus (LSDV)		Mechanical	Cattle - endemic to southern, central, eastern and western Africa	Skin infection Lethal - low mortality rate	(Baldacchino et al., 2013; Sohler et al., 2019)
Vesicular stomatitis (VS)	Vesicular stomatitis virus (VSV)		Mechanical	Horses, other equids, cattle, swine, llamas - endemic to the Americas	Mucous membrane infection Lethal	(Baldacchino et al., 2013; McCluskey and Mumford, 2000)
Anthrax	<i>Bacillus anthracis</i> Bacterium	<i>S. calcitrans</i>	Mechanical	Zebras, horses	Lymphatic tissue and spleen infection Lethal - high mortality rate	(Baldacchino et al., 2013; Radcliffe and Osofsky, 2002; Turnbull, 2008)
Bovine anaplasmosis	<i>Anaplasma marginale</i>	<i>S. calcitrans</i>	Mechanical	Cattle, horses [30]	Red blood cell infection Lethal - mortality rate 29-49% in adult cattle	(Baldacchino et al., 2013; Hungerford and Smith, 1996; Aubry and Geale, 2011; Leblond et al., 2005)
Nagana (trypanosomiasis)	<i>Trypanosoma congolense</i> , <i>T. vivax</i> and <i>T. brucei</i> Kinetoplastida (protist)		Mechanical	Equids, cattle, warthogs, antelope, African buffaloes and many others	Blood parasite/infection Lethal - mortality rate as high as 50-100% with some strains	(Baldacchino et al., 2013; Desquesnes et al., 2013; Anonymous, 2009)
Surra (trypanosomiasis)	<i>Trypanosoma evansi</i> Kinetoplastida (protist)	<i>S. varipes</i> <i>S. niger niger</i> <i>S. taeniatus</i>	Mechanical	Equids, camels, cattle and many others	Blood and tissue parasite/infection Lethal - often fatal	(Baldacchino et al., 2013; Desquesnes et al., 2013)
Bovine besnoitiosis	<i>Besnoitia besnoiti</i> Protozoan	<i>S. calcitrans</i>	Mechanical	Horses, donkeys, cattle	Skin, mucous membrane and conjunctiva infection Lethal - low mortality rate	(Baldacchino et al., 2013; Sellon and Long, 2013; Bigalke, 1981)
African swine	African swine	<i>S. calcitrans</i>	Mechanical	Pigs, wild	Lymph node	(Baldacchino

fever (ASF)	fever virus (ASFV)			boar, warthogs	infection Lethal - high mortality rate in naive populations, rate decreases with time	et al., 2013; Costard et al., 2013)
West Nile fever (WNF)	West Nile fever virus (WNV)		Mechanical	Horses and others (mainly birds)	CNS neurons infection Lethal - mortality rate 38-57.1% in horses	(Baldacchino et al., 2013; Castillo-Olivares and Wood, 2004)
Blue tongue disease	Blue tongue virus (BTV)		Mechanical	Sheep, cattle and other ruminants	Lymph node, phagocyte, lymphocyte and endothelial cell infection Lethal - up to 30% mortality	(Baldacchino et al., 2013; Maclachlan et al., 2009)
Habronemosis	<i>Habronema microstoma</i> and <i>H. muscae</i> Nematode	<i>S. calcitrans</i>	Biological	Horses	Stomach mucosa infection Not lethal - sores usually regress by winter (hence name 'summer sores')	(Baldacchino et al., 2013; Traversa et al., 2007)
Rift Valley fever (RVF)	Rift Valley fever virus (RVFV)	<i>S. calcitrans</i>	Mechanical	Sheep, cattle, goats and other ruminants	Liver infection Lethal - up to 100% mortality of young sheep, 20-60% for older sheep, and 90-100% of pregnant ewes abort	(Baldacchino et al., 2013; Pepin et al., 2010; Meegan and Bailey, 1989)

Future directions

In this review we have tried to address implicit assumptions about the premise that biting flies, particularly tabanids, are the evolutionary driver of striping patterns in zebras. There is abundant evidence to support this but four issues need to be addressed next. First, biting flies being thwarted by striping patterns is a robust finding based on multiple observational studies of zebras, artificial stimuli, models, coats and even other species but the extent to which these effects generalize across tabanid species, or diptera or other groups of flies is unknown and should be the subject of future studies.

Second, there are at least three candidate mechanisms by which stripes stymie landing attempts by tabanids, only one of which has been definitively rejected at time of writing – the aperture effect. The other hypotheses need urgent testing.

Third, there is strong evidence that tabanid, glossinid and *Stomoxys macro* and microgeographic ranges overlap with those of all three species of zebras. The length of time during the year that these three groups of ectoparasites are active is substantial, in many cases cover the whole year. There is no question that these flies bother zebras.

Each of these groups of flies carry diseases fatal or debilitating to zebras but whether zebras can develop immunity and to which diseases is unknown. Moreover, the extent to which different species of biting flies carry each sort of disease is unknown as is the geographic distribution of diseases across the African continent. Certainly, localized prevalence of some of these diseases such as trypanosomiasis in certain valleys but not others has been documented. However, research on this topic is notoriously difficult (Auty et al., 2008; Auty et al., 2012) but it is a necessary step in reinforcing the case for biting flies being the evolutionary driver of zebras' extraordinary coloration.

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