Insect ectoparasites: A driving force in the evolution of zebra stripes

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Abstract: Zebras are well-known for their distinctive striping pattern. The presence of contrastive white and black stripes has been attributed to camouflage, predator avoidance, thermoregulation, social interaction, and ectoparasite avoidance. According to latest studies, the stripes on zebras are essentially evolved to ward off biting flies. The presence of alternate black and white stripes causes the disruption of optic flow patterns, preventing the flies from landing. Flight trajectory studies also revealed the failure of landing by the biting flies particularly, tabanids. Evolutionary models have also confirmed the distribution of striped equids and biting flies. Striping characteristics such as thickness, number of stripes, and so on has also been treated to prevent biting flies. The genesis of zebra stripes has significance in animal husbandry as well.

Key words: Zebra stripes; Polarotactic tabanids; Evolution of stripes; Painted cows; African equids; Biting flies

Adopting any distinctive structure or behaviour in living creatures makes sense only when regarded as a series of evolutionary adaptations to specific selection pressures, implying that evolution is the cornerstone of biology and is fundamental to comprehending structural adaptations in the organisms. Likewise, zebras are several species of African equids united by their distinctive black-and-white striped coats. The unique stripes of zebras make them one of the animals most familiar to people. Their stripes come in different patterns, unique to each species, sometimes to subspecies also. As these contrasting black and white stripes are not found in other mammals, they are likely to have unique functions. Zebras have evolved among the Old-World horses within the last 4 million years (Azzaroli, 1992). It has been suggested that zebras are paraphyletic and that striped equids evolved more than once. However, molecular evidence supports zebras as a monophyletic lineage (Cirilli *et al.*, 2021). Zebras occur in an array of habitats, such as grasslands, savannah, woodlands, thorny scrublands, mountains, and coastal hills. The earliest report concerning the functional explanations for the stripes was started with Wallace who suggested that zebras have developed the striped coats as camouflage against carnivores in tall grass. Later, Darwin criticized his hypothesis with an explanation that zebras do not occur in such areas with dense vegetation but rather prefer open savannah habitats with short grass.

What could be the actual driving force for the evolution of stripes in zebras…?

The mysterious role of zebras' conspicuous black and white stripe pattern has been the focus of vigorous thoughts among researchers ever since Wallace and Darwin.

The meticulous functional explanations for these stripes were cloudy till the 19th century. Advanced studies related to the stripes function have given different explanations. There are 18 functional explanations suggested for the evolution of stripes in Zebras which can be folded into five main themes. These are camouflage, predator avoidance, heat management, social interaction, and avoiding ectoparasite attack (Horváth *et al*., 2018; Caro, 2020).

Camouflage is the eldest conception argued over by Wallace and Darwin. Early idea about the evolution of stripes was a form of crypsis/ camouflage to escape from the predators. Camouflage against predators may be expressed through background matching or else by disruptive colouration (Caro *et al.*, 2014). The recent evidence voices decisively contrary to this idea because a) Zebras are widely distributed in open plains of Africa (Savannah habitats) b) large carnivores can resolve stripes very easily and c) experiments showed that zebra stripes are quite noticeable to human observers (Caro *et al*., 2020; How *et al.*, 2020). Hence, camouflage could not be a major driving force for the evolution of stripes. It sometimes refers to avoid being killed by predators through the confusion by misjudging the number of zebras in the group, the size of the target, flight speed, or through quality advertisement or aposematism (Caro *et al.,* 2014). Observations made on plains zebras which are escaping did not corroborate theories that stripes confuse predators in ways that do not enhance protean behaviour, nor obscure the outline of individual animals, and because they do not promote motion dazzle or cause lions to misdirect their attack (Caro, 2020). The worst part is that lions killed zebras in numerous numbers than expected based on their abundance in 40 study sites across Africa, implying that confusion is a doubtful operational explanation for stripes (Hayward and Kerley, 2005; How *et al.,* 2020). The other assumption was that stripes were meant to assist mutual grooming and thereby encourage social bonding. However, mutual grooming is not frequent anymore in striped than non-striped equid species. Given that unstriped domesticated horses (*Equus caballus*) clearly recognize each other, the argument that stripes are employed for individual recognition appears dubious. Furthermore, equid species that live in loose social groupings where individual difference is important do not have stripes (Caro *et al.*, 2014; Caro, 2020).

Zebra stripes are also thought to cool the body by forming convective air eddies across alternating black and white stripes due to the temperature disparities. According to the thermoregulation hypothesis, upwelling air streams originate over the warmer black stripes, which are then replaced by cooler air from the nearby white stripes with downwelling air flows (Horváth *et al*., 2018). Some glitches with this hypothesis are portrayed as follows: i) Hitherto, convective eddies formed over zebra bodies have never been recognized. Typically, these buoyancy-driven eddies form only on the horizontal regions of zebras' striped body surface. Upwelling turbulent airflow could build over the sharply sloped or vertical sections of the body, such as the flanks, avoiding periodic eddies. Black stripes, on the other hand, are detrimental to the slanting and vertical side areas, as well as the legs, because of their strong light absorption. It is vital to remember that zebras must be striped only on their dorsal surface, not all over their bodies, if they are to execute thermoregulation; ii) Convective eddies over horizontal surfaces are not well-known for their stability. The feeble local breeze, which is always present in bright conditions, might easily blow eddies away. Furthermore, these eddies could be quickly disrupted if the zebra moves (Caro *et al.*, 2014); iii) Herbivores sympatric with zebras that live in the same microhabitats also require thermoregulation yet they are not striped. Other equid species, such as horses, ass, *etc*., which live in hot climates, are also not striped (Caro *et al*., 2014).

Furthermore, it is unclear if convective eddies over a weeping horizontal surface of a striped coat have a greater cooling effect than sweat cooling over any monochromatic garment (Caro *et al.*, 2014; Caro, 2020). Additionally, the arena experiments which were conducted to investigate the functional explanation of stripes for thermoregulation by using water-filled metal barrels covered with horse, cattle and zebra hides of various colours such as black, white, grey and striped patterns revealed that there is no significant difference between the striped and grey barrels, even on many hot days. When the zebra-striped coats do not retain the body cooler than the grey coats, which implies that there is no correlation between thermoregulation and the presence of black and white stripes (Horváth *et al*., 2018).

Do stripes mean thwarting biting flies...?

Despite an adjoining perspective that zebras have thin pelage compared to other African ungulates, the equids outside of Africa have seasonally thick coats to combat the impact of low temperature (zebras which are distributed across Europe). Biting flies are very problematic for equids and they can pierce their mouthparts easily through the thin coat and skin of equids. The major parasites of zebras are tsetse flies, stable flies (*Stomoxys* sp), and tabanid biting flies, which are known to carry a range of diseases such as trypanosomiasis, equine infectious anaemia, African horse illness and equine influenza, which are fatal to zebras (Caro, 2020). The inkling that stripes oblige to thwart biting flies from landing started in the 1940s and has since been tested with various artificial targets independently in both field and laboratory settings. Among all postulates advanced so far why zebras have stripes, the avoidance of biting fly attack takes the most support (Caro *et al.*, 2014).

Mechanism of avoiding biting flies:

The evolutionary cause of zebra stripes is now widely accepted as avoiding attack by biting flies. However, the exact mechanism by which stripes protect against ectoparasite attack was unknown (Caro *et al.*, 2019). According to recent studies, stripes impede with the optic flow patterns necessary for tabanids to execute precise landings. Optic flow is the pattern of apparent motion caused by relative movement between an observer (Fly) and the scene (Zebra). The striped patterns, in particular, can disrupt optic flow by interfering with the radial symmetry of developing optic flow fields through the aperture effect of uniformly spaced stripes (i.e., production of false motion cues by straight edges) (How *et al.*, 2020). It is mainly due to the degree of polarization generated by black and white stripes. Black stripes exhibit highly polarized light with a high degree of polarization, whereas white stripes reflect light with a much lower degree of polarization diffusely backscatter light. White stripes disrupt the degree and angle of an otherwise attractive black pelage polarization signature. As tabanids and possibly glossinids can detect polarized light, but are unable to resolve the unpolarized light (Horváth *et al*., 2017; Egri *et al*., 2012; Britten *et al*., 2016; Caro *et al*., 2014; Caro, 2020).

Functional explanations for zebra stripes:

For nearly a century, the purpose of zebra stripes has never been thoroughly investigated. In multifactor models, Caro *et al*. (2014) compared accord discrepancy in the striping of equid species and subspecies to geographic range intersect of environmental variables. Association between the measure of striping and environmental factors (Camouflage, predator avoidance, thermal cooling and avoiding parasitic attack) was assessed at species and subspecies levels with different regions of interest (flank and rump striping, leg stripe intensity, facial and neck stripe number and shadow striping) by giving importance score to each environmental factor to highlight the prominence of stripes. At both species and subspecies levels for a different region of interest, avoiding tabanids (ectoparasites) received the highest importance score, which put forward those stripes have a role in thwarting biting flies.

However, phylogenetic analysis of equid subspecies, leg stripe intensity and tabanid activity indicated that the leg stripe intensity of equids is directly proportional to the avoidance of tabanid activity. It also highlights that those striped equids are better distributed in African countries than Europe. African equids have thin coat/ skin (due to temperature factor); hence they suffer the nuisance of tabanids. To overcome this menace, equids which are distributed across Africa evolved the white stripes (Caro *et al*., 2014).

Do stripe parameters influence the avoidance of biting flies?

The stripe parameters such as the number of stripes, horizontal and vertical stripes, the direction of polarization produced by the stripes and the thickness of the stripe may influence the ectoparasite activity. Egri *et al*. (2012) conducted various experiments at a Hungarian horse farm at Szokolya to investigate the influence of stripe parameters and polarization generated by them on the tabanid activity. The experiment concluded with the following results, i) the amount of tabanids captured was reduced as denser the white grid on white framed black plates filled with salad oil; ii) as the number of stripes increased, more the number of tabanids avoided; iii) as the thickness of white stripes reduced, greater the tabanids avoided; iv) the attractiveness of tabanids is influenced by the direction of polarization, regardless of the direction of striping and, v) stripes (horizontal or vertical) with the same brightness and colour but with alternating orthogonal directions of polarization are less preferred by tabanids than similar polarizing surfaces with a constant direction of polarization. The study with three-dimensional horse-shaped targets with different colour patterns (brown, black, white and a black-and-white zebra-striped) revealed a significant difference in the number of tabanids attracted to these horse models. Remarkably, fewer individuals are trapped with zebra-striped horse models than other horse models (Egri *et al*.,2012).

The behaviour of tabanids such as their landing, touching and hovering performance around the uniformly coloured domestic horses and captive plain zebras were examined in three different sets of studies such as direct observational, other coloured coatings and flight trajectory studies (Caro *et al.,* 2019). The experiment concluded that i) there was no significant difference in the frequency of circles and touches made by tabanids between zebras or horses. However, concerning landing, there was a significant difference between zebras and horses with more bias towards horses; ii) the touching and landing rates were tilted more towards monotonously coloured horses than the striped horses. In contrast, no significant differences were observed in the sum of flies that landed on horses' naked heads as they were not covered with any coat and iii) a significantly greater proportion of tabanids touched zebras as compared to horses. In contrast, a significantly lower proportion of tabanids landed on zebras than on horses.

The practical implications of the evolution:

Biting flies are solemn pests of livestock that cause economic losses in animal production. Kojima *et al.* (2019) anticipated that cows with black and white stripes on their bodies may avoid being bitten by flies and also displayed some fly-repelling behaviour. The experiment conducted on six Japanese Black cows assigned with different treatments such as black & white painted stripes (B&W), black painted stripes, and no stripes (all-black body surface) showed that the total number of biting flies on the legs, body, and the sum of both parts of B&W cows were almost equal to half of those number on the control- and black striped cows. The lower fly-repelling behaviour was observed in B&W cows which were convened by the fewer numbers of biting flies on their legs and body (Kojima *et al.*, 2019).

Zebra related interesting facts!!!

1. We might have observed a typical body painting pattern of different tribes living in Africa and Australia (Horváth *et al.*, 2019). Tribes generally dwell in the forests, where they are troubled by blood-sucking ectoparasites such as horseflies. Finally, we are perplexed as to whether tribes were aware of the scientific rationale for the practice of striping to avoid parasite assaults.

2. Further, other insects like the Colorado potato beetle, Hissing beetle (*Polyphylla decemlineata*), red cotton bug, *etc*., are also with different stripes on their body. Whether they also have the same evolutionary relationship to combat their natural enemies is unsolvable. However, in some insects like the red cotton bug, it is known that white stripes are formed by the accumulation of uric acid.

Conclusion:

Except for the ectoparasites, other possible functional hypotheses behind zebra stripes such as camouflage, predatory avoidance, decreasing thermal load, and social function, are still unconvinced and lack experimental data. Stripes with brightness and polarization modulations interrupting the homogenous pattern of reflected light may have evolved as a selective advantage in evading polarotactic biting flies. Apart from polarotaxis, more research is needed to uncover the possible processes of thwarting. Evolution is a two-way process in which both entities engage with one another to counteract each other's defense systems; however little information is linked to tabanid evolution concerning zebra striping. Finally, it is amazing to know that a larger animal, zebras, evolved solely because of a little fly parasite called tabanids.

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