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**Author**

Pan, Vincent

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## Recent Advances in Elucidating the Function of Zebra Stripes: Parasite Avoidance and Thermoregulation Do Not Resolve the Mystery

### Introduction

Why are zebras striped? This question has baffled biologists for ages since the time of Darwin (Darwin 545). Although we remain far from an answer, past research was not done in vain. Currently, as much as 18 different theories have been proposed (Horváth et al. “EETSDNCZ” 1). These proposed explanations largely fall into four categories: 1) Predator avoidance through crypsis and various types of visual confusion (Ruxton 238), 2) reinforcement of social interactions (239), 3) ectoparasite deterrence (241), and 4) thermoregulation (239).

Among the four groups of hypotheses, only the latter two have gained some support. The speculations that stripes help zebras blend in with tall grass (238), appear larger when in a group (237), or dazzle vertebrate predators like lions or spotted hyenas (238) were all but rejected because of the lack of empirical support and not because of the lack of trying (Caro et al. “TFOZS” 3; Larison et al. “HTZGIS” 3; Ruxton 238). Similarly, the idea that zebra stripes provide social benefits such as individual identification and bonding remains largely speculative (Ruxton 240), if not just outright rejected (Caro et al. “TFOZS” 3). Many of the hypotheses also do not actually suggest a fitness benefit but explain how the zebras interact (Ruxton 239). Therefore, they insufficiently explain why zebra stripes evolved in the first place. In contrast, overwhelming empirical evidence support the hypothesis that ‘zebra like’ stripes deter ectoparasites like glossinids and tabanids (Blaho et al. 173; Brady and Shereni 302; Caro et al. “BOZS” 10; Egri et al. “PTFSPWBAPMLA” 740; Gibson 145; Horvath et al. “SBPAH” 9; Waage 354); at least some empirical evidence likewise supports the hypothesis that zebra stripes facilitate thermoregulation (Larison “HTZGIS” 4). The fly deterrence and thermoregulation function possess substantial

fitness benefits as well. Biting flies often carry a myriad of deadly diseases, many of which plague unstriped equids where zebras occur (Caro et al. “TFOZS” supplementary table; Larison et al. “HTZGIS” 4). Successful deterrence of these parasites therefore alleviates their strong selective pressure. The cooling effect of stripes can also increase zebra thermal tolerance. Under the grueling sun of the African savanna where shade is scarce, stripes may protect zebras from heat related illnesses.

Accordingly, it appears that both the fly deterrence and thermoregulation hypotheses have merit. Yet, our understanding of their mechanism and role in evolution remains convoluted at best. Many authors have reported conflicting results and publicized arguments appear common place (e.g. Caro et al. “TFOZS” 3; Larison et al. “HTZGIS” 6; Caro and Stankowich 1; Larison et al. “COZSINBAW” 1). Still, some challenged if either of these functions exist at all (Horváth et al. “EETSDNCZ” 9; Larison “HTZGIS” 4). Hence, this review summarizes and evaluates the arguments for and against the fly deterrence and thermoregulation hypotheses and examines the mechanisms that have been proposed for them thus far. In particular, the evolutionary benefit of zebra stripes in light of our recent renewed perspective of the two hypotheses is emphasized.

## **The Fly Deterrence Hypothesis**

### *The Fly Deterrence Phenomenon*

Starting from the 80s and 90s, experiments using striped models began to show that stripes attract less tsetse flies (glossinids) than their black and white counterparts (Waage 354; Brady and Shereni 302; Gibson 145). Subsequent studies in the 2010s focused on different species of horseflies (tabanids) too showed that striped targets are less attractive (Blaho et al. 173; Caro et al. “BOZS” 10; Egri et al. “PTFSPWBAPMLA” 740). More recently, some authors have shifted their

attention beyond zebras and either proposed or found similar results in other biological systems with ‘zebra like stripes’, such as in tabanid-human interactions (Horvath et al. “SBPAH” 9) and herbivore-plant interactions (Lev-Yadun 695). Taken together, the fact that multiple researchers have independently found that many species of biting flies avoid striped surfaces in various experimental conditions and setup indicate that the behavior of stripe avoidance is real and robust.

However, caution must be exercised when interpreting some of these results. At a distance, stripes simply appear grey to flies. For instance, Gibson and Young calculated the maximum resolvable spatial period of *Glossina pallidipes* at 3.5 degrees (Gibson and Young 280), meaning even the widest zebra stripes at 20 cm apart still require a maximum of within 3 meters for a fly to resolve the stripes (Gibson 146). Thus, at long distances, what determines a host’s palatability depends not on the surface coloration, but the hosts’ chemical cues. Perhaps the strongest support of this notion comes from Caro et al. They noted that tabanids spend similar amount of time circling striped and unstriped equids (“BOZS” 5); only when the flies are within two meters did the tabanids appear affected (10). As such, one cannot rule out that stripes are only an effective deterrent when zebras are near other unstriped, but similarly palatable hosts. In nature, this condition would be a difficult prerequisite to satisfy. Studies using a choice test (Balho et al. 169; Gibson 143; Egri et al. “PTFSPWBAPMLA” 738) design may therefore exaggerate the efficacy of stripes.

### *Mechanism of Fly Deterrence*

As an attempt to understand the fly deterrence mechanism, Caro et al. examined video footages of tabanids around striped equids. They discovered that tabanids failed to decelerate in the last half second before contact with host and consequently had a high likelihood of landing

failure (“BOZS” 11). Caro et al. remain agnostic regarding the mechanism but suggested that the stripes may disrupt the optical flow of the flies. If so, it would be unsurprising, as Dipterans are known to use an expanding image in their optic field as a signal for controlled landing (Srinivasan et al. 2752). Nevertheless, how stripes specifically disrupt this signal remains unclear.

Instead of the flies wrongly precepting their speed and direction, some authors have suggested that zebra stripes may also cause the flies to misinterpret their target’s speed and direction (i.e. motion dazzle) (Britten et al. 12). However, this hypothesis remains in question. Despite the compelling theoretical work offered by How and Zanker, which suggested that highly contrasting stripes may help zebras achieve motion dazzle through the wagon-wheel effect and barber-pole illusion, this hypothesis suffers from the lack of empirical support (167). Indeed, at present, only one study has tested the motion dazzle phenomenon in insects, and it was on an Orthopteran (Santer 2).

The polarized light hypothesis Horváth and his research group suggested is currently by far the most convincing, though still problematic. Multiple studies have reported that tabanids use linear polarized light to locate their host (Egri et al. “NKOPGBDOP” 414; Horváth et al. “WDHNPVFHD” 12), and some asserted that the alternating black and white zebra stripes reduces the polarized light signals and thus, a zebra’s attractiveness (Egri et al. “PTFSPWBAPMLA” 740; Blahó et al. 173). Egri et al. for instance, reported a striking difference in the level of polarization  $d$  between black stripes at values greater than 80% and white stripes at values below 5% when they measured museum zebra pelts in Hungary (“PTFSPWBAPMLA” 740). The same research group in a subsequent study found comparable numbers (Blahó et al. 172). In contrast, Britten et al. who measured live zebras in Africa reported a less than striking result: not only do the black and white stripes reflect comparable polarized light in terms of both the level and angle of linear polarization,

the polarized signal differs substantially from the background (12). Thus, polarized light-seeking tabanids would have no trouble picking out zebras. While Egri et al. did not commit any glaring methodological problem, their characterization of the polarized light is less than realistic. Britten et al. pointed out that museum pelts are often treated to preserve the color and are usually kept relatively free of dust (12); this differs greatly from the conditions of zebra coats in the wild, especially during the dry season when Britten et al. made their measurements. As such, these differences meant that Egri et al. may have exaggerated the characterization of polarized light. The mechanism they proposed may very well explain the fly deterrence phenomenon in studies using artificial zebra models, but it likely does not apply to zebras in natural conditions. Thus, this fact calls into question the validity of earlier studies that heavily relied on artificial surfaces.

### **The Thermoregulation Hypothesis**

Unlike the fly deterrence hypothesis, the mechanism of the thermoregulation hypothesis is self-evident from the start. Under the sun, the difference in absorbance between black and white stripes causes temperature gradients and as a result, convection currents may form (Ruxton 241; Horváth et al. “EETSDNCZ” 3). These rotary eddies enhance evaporative cooling by increasing the surface area in contact with the zebra skin.

What remains unclear, however, is whether the cooling effect has a non-trivial impact. Preliminary support of this phenomenon comes from researchers pointing a thermometer gun at zebras in the field and finding zebras maintain lower temperature than objects and animals in the vicinity (qtd in. Larison “HTZGIS” 4). The first experimental evidence comes from Horváth et al. who used striped and unstriped water barrels to simulate the core temperature of equids under the sun (“EETSDNCZ”). While Horváth et al. concede that convective eddies may have occurred (3),

they reported that the eddies were apparently not enough to make a difference, as the temperature of striped barrels stayed identical to their grey counterpart and in between that of the black and white barrels (5).

Indeed, some authors have suggested a wealth of reasons to be skeptical of the supposed cooling effect. Horvath et al. noted that convective cooling would only be effective under low wind speeds and high temperatures; however, the two appear to be highly correlated (2). Thus, eddies are likely to be blown away when the temperature gets hot enough to form. Even if no wind blew, zebra movements itself would likely have a similar effect (2). Moreover, because bounciness-driven currents can only form over a horizontal surface (2), it raises the question why a zebra's legs and belly are striped.

Regardless, one important caveat to keep in mind is that the barrels used by Horvath et al. do not sweat like real zebras do. Because the mechanism of the thermoregulation hypothesis works through enhancing the efficiency of evaporative cooling, with no attempt to emulate sweating, Horvath et al. did not adequately test the hypothesis. As such, with the study done by Horvath et al. being the only one to offer any sort of experimental evidence and the fact that anecdotal observations suggest that zebras are cooler than their surroundings, the thermoregulation hypothesis remains far from defeated.

### **The Ultimate Cause of Zebra Stripe Evolution**

Because direct measurement of the fitness benefit of zebras is impractical, researchers have resorted to using comparative studies to examine the role of stripes in evolution. Caro et al. made the first attempt. By comparing the morphological features of 7 species and 20 subspecies of equids according to their local biotic and abiotic conditions ("TFOZS" 7), Caro et al. found that tabanids

distribution explained the most morphological variation, whereas tsetse fly distribution explained only the belly stripe number and monthly maximum temperature explained none (3). They concluded that the fly deterrence function (4), instead of thermoregulation (7) probably have more relevance to fitness. In particular, the tabanids, rather than tsetse flies, exerted more selective pressure (Caro and Stankowich 3). However, more recently, Larison et al. in a similar comparative study of different populations of *Equus quagga* reported opposite findings. They found that temperature, not tsetse fly distribution, explained the variation in zebra phenotype (“HTZGIS” 4).

The difference between the two studies apparently lies in the interpretation of the temperature data. Caro et al. had used maximum daily temperature and humidity to (“TFOZS” 8) to estimate the range of tabanids, which Larison et al. object to for being inaccurate (“HTZGIS” 6). Larison et al. rightfully pointed out that using only two climate parameters with questionable reliability meant that lots of factors in addition to tabanids may explain the relation to equid morphology (“COZSINBAW” 2). Specifically, they suggested that temperature and to a lesser extent, humidity, may be in and of itself a more parsimonious explanation (1). Yet, the study of Larison et al. too is far from perfect. For instance, they did not perform phylogenetic corrections for subspecies. Like Caro et al., rather than using abundance data, Larison et al. also only modeled ectoparasite threats with presence-absence data, a poor indicator of biting fly risks. In addition, the fact that comparisons were only made within plains zebras meant that anything inferred only pertains to the evolution of *E. quagga*, not the genus that the evolution of ‘zebra stripes’ evolved. Nevertheless, both groups of authors agree to question the importance of tsetse flies (Caro and Stankowich 3).

## **Conclusion**



While current research does not give a definitive answer as to why zebras are striped, it appears to move collectively toward one direction. Since the last two decades, temperature and ectoparasites clearly emerged as part of the solution. Despite none of the studies are perfect, attempts at demonstrating the fly deterrence phenomenon were consistently fruitful, but the same cannot be said of the cooling phenomenon. If the proposed mechanisms offer any hint, it would appear that the thermoregulation hypothesis is more easily defeated just based on theoretical grounds alone. On the other hand, findings about polarized light and the subsequent challenge from Britten et al. call into question the results of past studies using zebra models, as polarized light may be at work in simulated conditions but not in the wild. The recent work of Caro et al. that used live zebras is the only exception. However, because the zebras were captive in the United Kingdom (2) and thus presumably relatively free of dust, it remains unclear if only light polarization explained the result. Still, the support for the fly deterrence hypothesis easily overwhelms that of the thermoregulation hypothesis.

The strongest support for the thermoregulation hypothesis comes from the two comparative studies by Caro et al. and Larison et al. Although, the prerequisite of such an interpretation is that the cooling effect does exist, which by all indications appears questionable. As such, the interpretation that the comparative studies support the fly deterrence hypothesis appears to be the most consistent with current knowledge. Nonetheless, the reality is probably more nuanced. Larison et al. recognized that the flies are probably less important than the diseases they transmit, and that temperature can impact disease infection rates (“HTZGIS” 5). Concordantly, past researchers working on biocontrols have learned that the pathogenicity and virulence of a pathogen often depends greatly on the temperature (Thomas and Blandford 345). Realistic small fluctuations in temperature can drastically change the outcome of introducing a pathogen (345). Thus, it may

not be surprising that temperature is a stronger predictor than fly distribution. Future research should focus on elucidating the effect of temperature on the dynamics between flies, zebras, and their pathogens.

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