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WHAT IS THE TRUE PURPOSE OF ZEBRA STRIPES: A REVIEW

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Summary

Coloration has been studied in different species across the animal kingdom and has been shown to be important for several mechanisms, such as sexual selection and survival in mammals and birds. The zebra's striking black and white striped pelage has intrigued people for centuries and has captured the attention of many biologists, but its evolutionary origins and adaptive significance remain unsolved. Currently, as much as 18 different theories have been proposed for striping in zebras. Functional hypotheses fall into four broad categories: 1) camouflage against predators; 2) thermoregulation; 3) reinforcement of social interactions; 4) avoidance of ectoparasite attacks – „the ectoparasite hypothesis“. A consensus is emerging among biologists regarding the function of the black and white striped pelage of zebras, which supports the ectoparasite hypothesis. This hypothesis suggests that stripping in the pelage of zebras is an evolutionary response to ectoparasitic burdens, specifically biting flies, because such stripes inhibit their vision system. However, the exact mechanism by which stripes prevent flies from feeding on blood is not as well understood. This article reviews the major hypotheses for zebra striping and evaluates the growing consensus around the ectoparasite hypothesis, while highlighting the need for further empirical research to fully understand the underlying mechanisms.

Key words: zebra, black and white striped pelage, camouflage, thermoregulation, ectoparasite hypothesis.

1. Introduction

The study of coloration in animals has been popularized in the time of Darwin (1871) and Wallace (1891) and since then has been attracting the attention of many other scientists (Smith, 2020). Coloration has been extensively investigated across diverse taxa within the animal kingdom, demonstrating significant roles in multiple biological mechanisms, including sexual selection and survival strategies in mammals and birds. (Connock, 2020).

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The zebra's (*Equus quagga*) striking black and white striped pelage (Figure 1) has intrigued people for centuries and has captured the attention of many biologists, but its evolutionary origins and adaptive significance remain unsolved (Caro et al., 2014). Pelage is usually defined in zoological terms as the wool, fur or hair of a mammal (Smith, 2020). This trait is rare, intensely expressed, and noticeable, so an adaptationist explanation seems to be needed. However, the utility of a complete coat of densely packed, sharply contrasting black-and-white stripes is not immediately obvious. So, the stripes represent an ideal evolutionary puzzle: a trait that is so subtle that it seems like it must be "for" something, but which gives no clear advantage to its bearers and imposes obvious costs as visibility (Caro et al., 2014; Tombak et al., 2022).

Figure 1. Photograph of *Equus quagga* from Lake Nakuru National Park in Kenya, East Africa (orig.).

Currently, up to 18 distinct hypotheses have been proposed to explain the presence of striping in zebras. These functional hypotheses can be broadly categorized into four main groups: 1) thermoregulation, suggesting that the stripes help reduce heat load and facilitate cooling of the animal; 2) social functions, including roles such as individual recognition, promoting group cohesion, stimulating social interactions among conspecifics, influencing sexual selection, or

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directing grooming behavior to specific body regions; 3) camouflage mechanisms, which encompass aposematic (disruptive) coloration that may confuse predators by distorting perceptions of group size, target size, movement speed, or by blending with the background environment; and 4) avoidance of ectoparasite attacks, known as the ectoparasite hypothesis. These theories have been explored and supported by various studies (Connock, 2020; Caro et al., 2014; Larison et al., 2015; Pan, 2020; Tombak et al., 2022).

2. The most popular theories for striping in zebras.

2.1. Purpose of Zebra Stripes: Function as a Thermoregulatory Mechanism

The ability of zebras to maintain a constant body temperature is influenced by both their basic biology as equids and the environment in which they live. Plains zebras living at high altitudes on the Equator experience temperatures that can rise to at least 40 °C during the day and sometimes drop to below freezing temperatures at night (Cobb and Cobb, 2019). It has been observed that zebra's fur is affected by the cold and in the morning at sunrise the black stripes are a bit colder than the white ones. At that time of the day the hairs of the white stripes remain flat while the black hairs piloerect as a reaction to the cold. Piloerection of the black hairs can also be noticed during the hottest part of the day around after noon time, presumably as a cooling mechanism (Cobb and Cobb, 2019).

In one research data shows that once the sun is up and shining right on zebras a relatively constant temperature difference (of 12-15 °C) between black and white stripes is established and maintained for the next few hours (Cobb and Cobb, 2019). Some researchers suggest that the different temperatures placed side by side may cause convective airflow across the surface of the hair, with warm air rising from the warmer (black) stripes and cool air descending to the cooler (white) stripes (Ruxton, 2002; Horváth et al., 2018). On the surface of the fur of living zebras, temperatures are more stable and lower (never exceeding 56 °C for the black stripes) than on a lifeless fur, which may reach temperatures of over 70 °C (Cobb and Cobb, 2019). This suggests that living zebras may have some other mechanisms that help them to suppress overheating. For instance, like all other equines, zebras can and do sweat to keep themselves cool (Jenkinson et al., 2006; Horváth et al., 2018). It is important to note that it is not the sweat that cools the animal, but

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it's evaporation. This explains why zebras tend to avoid living in humid climates. Zebras can also pant, but they usually do only after exertion (Jenkinson et al., 2006).

Many researches show that there is no special capillary circulatory system under the skin of zebras to aid cooling (Cobb and Cobb, 2019). Scientists have studied a zebra's pigmentation and cutaneous vasculature by using radio-opaque dye perfusion, X-rays and infusion of the skin with latex and colloid carbon. Their results show no difference in the distribution and the anatomic structure of cutaneous vasculature between the black and white striped skin (Cobb and Cobb, 2019). Unlike giraffes, no anatomical adaptations to skin circulation, such as rete systems, have been found in zebras. (Cobb and Cobb, 2019). This leads to the conclusion that zebras do not use a counter-current heat-exchange mechanism to cool themselves, as do giraffes (Jenkinson et al., 2006; Horváth et al., 2018; Cobb and Cobb, 2019).

2.2. Zebra Stripes and Social Interactions

Plains zebras are sociable equine animals that rely heavily on group cohesion throughout their lives (Smith, 2020). A polygynous system is observed. A polygynous mating system means one sexually active stallion with several females in a harem-type group. Typically, a harem is expected to have up to eight adult females (Smith, 2020). The stability of the group is considered an important aspect of social cohesion. Plains zebras have a multi-level social system (Rubenstein and Hack, 2004). Multi-stratified societies consist of a two-tiered system in which the harem (the primary breeding group) is the first tier, and the herd is the second tier (Rubenstein and Hack, 2004). Herds typically contain several harems (Smith, 2020). Unlike many noticeable visual traits, striped pelage is expressed in both sexes with comparable intensity and is thus unlikely to have arisen through sexual selection alone (Tombak et al., 2022; Caro et al., 2019).

Behavior and social relationships are important in the life of the plains zebra. There are some hypotheses that support that stripe patterns influence some social factors. It is assumed that social interactions, such as grooming, favor animals that have stripes (Ruxton, 2002). This suggests that stripes are used as visual markers that direct conspecifics to specific parts of the body (neck and mane) for grooming, thereby promoting mutual grooming and social bonds (Ruxton, 2002). However, no correlation has been observed between the number of stripes and social interactions.

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This refutes the hypothesis that stripes are used as visual markers for cleaning and grooming (Melin et al., 2016; Smith, 2020).

Individual identification is also a proposed hypothesis, which claims that zebras can identify individuals by their unique patterns. Plains zebras have been observed searching for lost members of their herd, proving that individual identification is evident (Smith, 2020). The bond between a mother and her foal is an example of recognition found in all equids. However, there are studies that support the thesis that wild horses have the same identification mechanisms even without stripes on their coat (Smith, 2020). Individual recognition can also be observed in domestic horses. It has been established that domestic horses use both olfactory and vocal and visual recognition to identify individuals in their social group. This information, which applies to other horse species, refutes the hypothesis of personal recognition based on the stripe (Melin et al., 2016; Smith, 2020).

2.3. Zebra Stripes vs. Predators

Zebras are a species that stands out as one of the most prominent bearers of what can be interpreted as dazzle patterns (Ruxton, 2002; How and Zanker, 2014). The black and white stripes of zebras are extremely contrasting. Dazzle patterns are patterns that have the ability to confuse observers, and in particular threatening agents such as predators (How and Zanker, 2014). These deceptive patterns are proposed to hinder the detection and pursuit of moving targets by misleading observers about their location, shape, or movement (Stevens, 2007; Stevens et al., 2008). Relatively few mechanisms have been proposed for how exactly this protection can be implemented, due to the obvious visual conspicuousness of zebras in the African savannah, at least to the human observer (Stevens, 2007). Suggestions include that stripes somehow confuse observers or make zebras appear larger (Ruxton, 2002; Stevens, 2007). Stripes are obviously not aposematic warning signals, nor do they provide camouflage in either the savannah or woodland habitats common across zebra ranges (Tombak et al., 2022; Caro et al., 2019).

There is some empirical support in humans that deceptive patterns can lead to incorrect estimation of perceived speed or obscure the direction of motion (Stevens et al., 2011; Scott-Samuel et al., 2011). It is well known that several different forms of optical illusion are generated when periodic stripe patterns are combined with movement (Zanker et al., 2010). Some of these

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are the wagon-wheel effect (Pakarian and Yasamy, 2003) and the barber-pole illusion, which is based on the aperture effect (How and Zanker, 2014).

In some Western movies, the wagon wheel effect (Figure 2) can often be seen. In the stroboscopic presentation of a film sequence, where a series of still images are displayed in rapid succession, creating the illusion of continuous motion, a slowly rotating wagon-wheel can be seen to rotate in the correct direction. However, when the rotation speed exceeds a certain threshold value, the wheel appears to change direction or stand still (How and Zanker, 2014). This phenomenon occurs because above certain speeds each spoke of the wheel correlates with the previous spoke, instead of each spoke correlating spatially with itself in time. This leads to a reversal of the perceived direction of movement (How and Zanker, 2014).

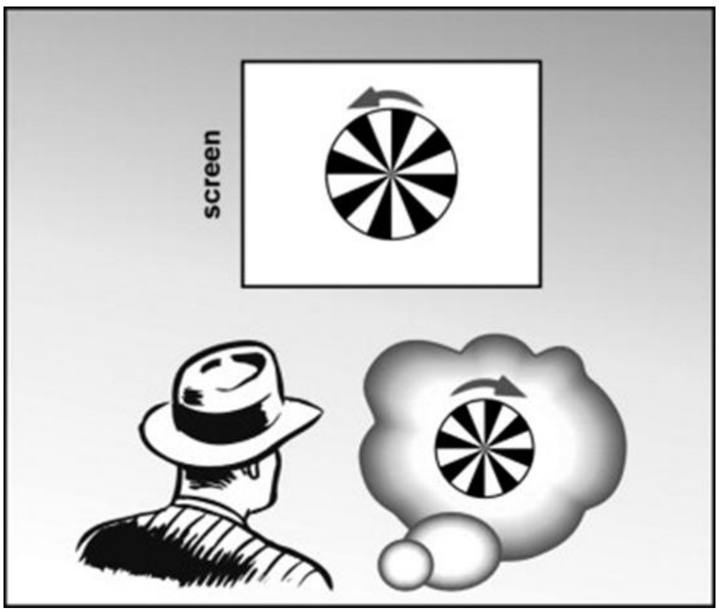

Figure 2. The continuous Wagon Wheel Illusion. A periodically moving stimulus (e.g., a rotating wheel) might be misperceived even under continuous illumination (sunlight). One interpretation of this phenomenon is, thus, that the visual system itself perceives information in discrete frames. Alternative explanations rely essentially on neuronal adaptation (source: VanRullen, 2007).

The barber pole illusion is a visual trick in which diagonal stripes on a rotating cylinder appear to move vertically (up or down) instead of rotating around the cylinder, as they actually do. The illusion is named after the advertising signs of barber shops, which represent a vertical white

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pillar rotating around its vertical axis, on which a spiral motif of alternating blue, white and red stripes is painted (How and Zanker, 2014). Even though the colored stripes move horizontally in the visual field, they locally appear to move upwards along the edges or in a direction perpendicular to the orientation of the painted stripes. This often gives the general impression of a dense upward movement of the barber-pole (Troscianko et al., 2009; How and Zanker, 2014).

Most large African carnivores have forward-facing binocular vision (How and Zanker, 2014). They also have a very well-developed visual tracking system designed to keep moving objects and running prey in the central part of the fovea. A horizontal saccade is a rapid, coordinated eye movement that shifts the gaze from one point to another horizontally. This saccadic eye movement is a common oculo-motor feature of active vision systems in animals (How and Zanker, 2014). When such a horizontal retinal displacement occurs, similar to the wagon wheel effect, the vertical stripes in the flank region can generate motion signals in the opposite direction of the actual movement. Also, similar to the barber-pole illusion, the diagonal stripes of the rump region of the animal elicit motion signals 50–60° away from the actual movement direction (How and Zanker, 2014). The impact of these erroneous motion cues is most intense when observing several animals naturally moving together in a herd. It is well known that groups of zebras gather together to form a tight herd when they are endangered by predators (Smith, 2020). In such a real-world stimulus, each animal creates a complex mixture of motion information by generating motion signals in different directions. In addition to the motion confusion, the configuration of the group further hinders the separation of individual zebras, even when they are moving at different speeds or directions. It's also creating difficulties in assessing each individual's over-all direction of movement (How and Zanker, 2014).

It's speculated that both of these illusions confuse the motion perception system of the real observer, representing a potential predator avoidance mechanism (How and Zanker, 2014). This dazzle camouflage could be interpreted as an evolutionary explanation of the zebra's fur pattern as a means of confusing predators about the prey's movement (Stevens et al., 2008; Scott-Samuel et al., 2011). A discussed crucial aspect of the dazzle camouflage is interference with segmentation mechanisms and localizing targets (Troscianko et al., 2009).

Zebras just like other uniformly colored equid species are conspicuous in the plains because their body silhouette has a high brightness contrast against the sky. Current data suggest that in

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open plains – an environment in which zebras spend much of the year, stripes do not disrupt body contours (Ruxton, 2002). Therefore, the black and white striped pelage of zebras may not confer any advantage over species without stripes. In some wooded environments, to most of the predators, under many conditions zebras appear grey (Ruxton, 2002; Melin et al., 2016). In such environments, the stripes might resemble branches and small tree trunks, but they can only be distinguished by nearby predators (Melin et al., 2016). In a woodland habitat only a stationary, silent nearby zebra can take advantage of the camouflage due to stripes, at a distance at which scent could be a cue to predators. Zebras might be even noisier in woodland than grassland habitats, because of the branches under their hooves. And so, the chances of zebra prey remaining hidden when near to a predator are minimal (Melin et al., 2016).

2.4. Purpose of Zebra Stripes: Ectoparasite Hypothesis

Zebras, like most ungulates, are attacked by tabanids, glossinids, stomoxyds and other biting flies, which can inflict significant blood loss, transmit various infectious and prozoal diseases, and weaken the host's immune system (Hopla et al., 1994). Also, the fly-avoidance behaviors reduce the host's feeding rate and make it vulnerable to predator attacks (Tombak et al., 2022; Caro et al., 2019). In Africa where zebras live, tabanids carry diseases fatal to zebras including equine infectious anemia, trypanosomiasis, equine influenza and African horse sickness and zebras are particularly susceptible to infection because their thin pelage allows biting flies to probe successfully with their mouthparts (Caro et al., 2019; Hopla et al., 1994). However, they are attacked by flies far less than other equids (Figure 3), and less than other ungulates across their African range (Tombak et al., 2022; Caro et al., 2019). Zebras and some sympatric ungulates produce specific odors that may augment their anti-fly defenses but alone have no repellent effects (Tombak et al., 2022; Waage, 1981).

A consensus is emerging among biologists regarding the function of the black and white striped pelage of zebras, which supports the ectoparasite hypothesis (Caro et al., 2019). This hypothesis suggests that stripping in the pelage of zebras is an evolutionary response to ectoparasitic burdens, specifically biting flies, because such stripes inhibit their vision system (Connock, 2020; Caro et al., 2019). However, the exact mechanism by which stripes prevent flies from feeding on blood is not as well understood. Flies may fail to detect a zebra from a distance, or from close up, either as a result of misinterpreting optic flow as they approach, by disrupting

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the polarization signature of their host, or by interfering with cues that promote a landing response (Tombak et al., 2022; Caro et al., 2019; Egri et al., 2012).

Figure 3. Examples of horsefly flight paths around domestic horses and captive plains zebra. The red arrows indicate the direction of flight. The blue stars indicate the points of contact or landings on the equid. The blue arrows show the final position of the approach and initial position of the departure phases of flight (orig.).

Multiple lines of evidence indicate that stripes do not stop tabanids and other flies approaching from a distance, but more likely prevent effective landing by tabanids once they are in the vicinity of the host (Caro et al., 2019). Zebras also seem to use behavioral means to prevent tabanids spending time on them by constant wagging of their tail and even running away from them. As a consequence of both of these behavioral and morphological defenses, very few biting flies are able to probe for a zebra blood meal (Caro et al., 2019).

Many studies indicate that horseflies are attracted to zebras from a distance but are prevented from appropriate landing behavior near their target. Many detailed video analyses show that in comparison to horses proportionally more tabanids simply touch rather than land on zebra pelage. This is because flies approach zebras faster and fail to decelerate before contacting them (Egri et al., 2012; Caro, 2020; Caro et al., 2023). Regular patterns could become misregistered when viewed by the fly while in motion producing false motion magnitudes and directions. An example of which is the wagon-wheel effect for a human observer (Figure 2). Crucially this

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mechanism of misperception depends on the pattern's regularity (Caro, 2020; How and Zanker, 2014; How et al., 2020).

Many analyses speculate that black stripes, by nature of being thin, serve to minimize the size of local features on an equid target that are attractive to biting flies (Caro et al., 2023). The body location of the widest stripes varies among zebra species (Figure 4). The widest stripes are commonly on the flank, the neck or the rump of the zebra. The thinnest stripes for all zebra species are consistently on the forelimbs (Melin et al., 2016). Stripes may also be found on the legs of other species of the same genus (e.g., *Equus africanus).* Horseflies are attracted to equid hosts owing to a combination of factors such as odor at a distance, and the size of the animal contrasted against the sky or vegetation at a middle distance (Waage, 1981; Caro et al., 2023). But flies make a visual switch to local features at close range, where they can no longer see the body's outline. If they are small dark objects contrasted against a white or light background, the horsefly can no longer recognize them as a host target and veers away. An important component in preventing tabanid landings is the size of the dark object (Caro et al., 2023). Therefore, it is considered that the key elements of how stripes operate to thwart fly landings are the contrast of stripes and their relatively small size (Caro et al., 2023; Caro and Stankowich, 2015).

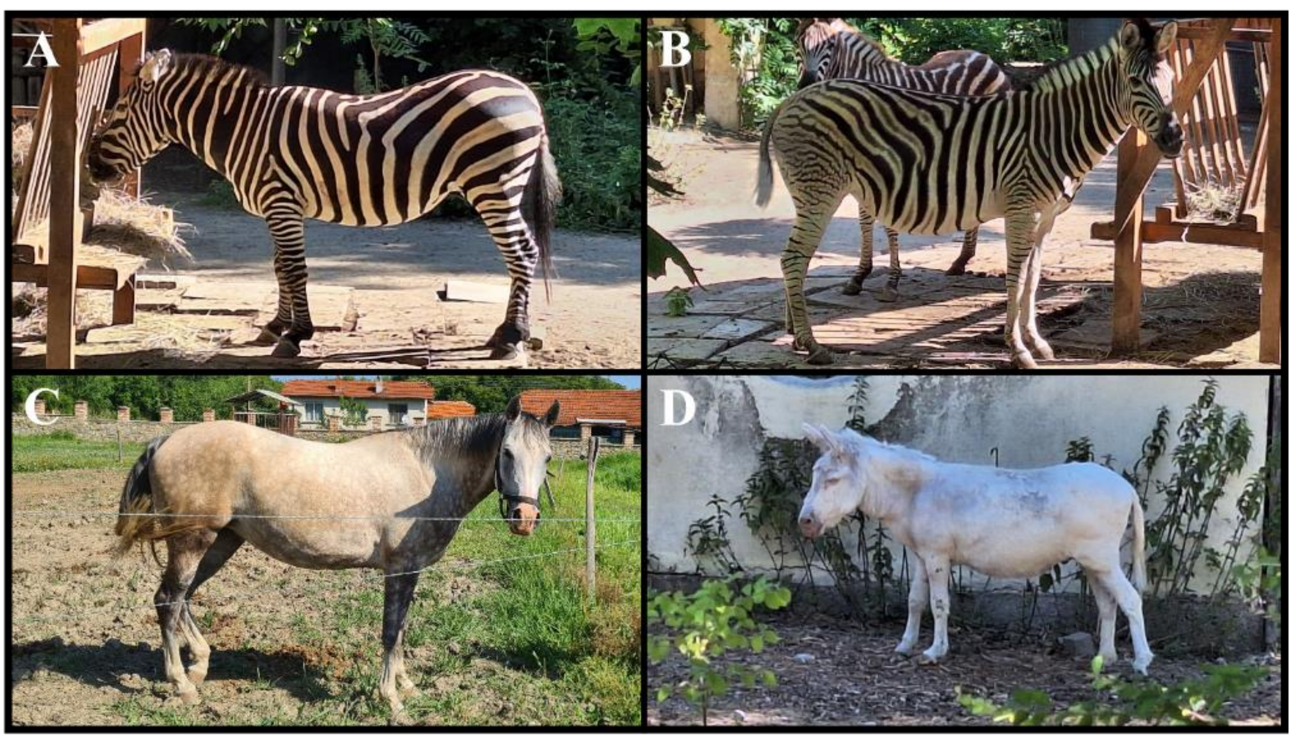

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Figure 4. Photographs of A) *Equus quagga*, B) *Equus quagga burchelli*, C) *Equus caballus*, and D) *Equus asinus* from Sofia Zoo, Bulgaria (orig.).

3. Conclusion

To elucidate the true functionality of striping in zebras needs much additional work. More realistic experimental studies are needed to investigate whether stripes function at close range creating optical illusions resulting in confusion and decreasing the likelihood of being predated or bitten, and whether they function at a distance to help zebra evade detection. The lack of parasite data in zebras may not be related to the characteristic of striping. While stripes obviously create confusion in the limited environment of the computer screen, the same phenomenon may not occur on a larger scale under normal conditions. Clearly, larger-scale experiments with live animals or a virtual system are needed. To investigate the potential role of temperature more experiments must be conducted. Whether stripes function in thermoregulation, how environmental factors influence ectoparasites and likelihood of infection if bitten, all need to be studied.

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