Why Does a Zebra Have Stripes?

(Maybe This Is the Wrong Question)

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It is hard not to be in awe of nature's creativity as expressed in the striped coat of zebras. The rhythmically sequenced, flowing, black-and-white bands of hair are formed as the zebra develops in the womb. Each of the three different species recognized today— plains zebra (*Equus quagga*), Grevy's zebra (*Equus grevyi*), mountain zebra (*Equus zebra*) — has a characteristic striping pattern. And yet there is considerable variation in the pattern in each species, and also among individuals. I'll focus on the plains zebra.

A Potent Pattern

When mesmerized by the overall impression of this striped animal, we may fail to perceive consciously what an organic work of art the striping pattern is. We can consider the striping pattern from the perspective of what I will call *biological aesthetics*: we look closely, moving through the details in such a way that their interrelations and connections with different features of the body and the animal's activity begin to show themselves. The descriptions that follow can only point to what needs to be experienced, so please look at the photos to fill out what the text hints at.

The striping pattern is most complex and refined in the zebra's head, where the senses of sight, hearing, smell, taste, and touch are centered. In the neck and head the animal has greatest freedom of movement—turning down to graze, moving up or from side to side to look and listen.

Between the eyes there are long narrow stripes that end in the dark snout; they broaden at the height of the eyes and narrow to the snout and again at the top of the head. The stripes curve around the eyes and the base of the ears. The side of the head has stripes that are perpendicular to the length of the head and curve to converge with those lengthwise stripes to create a wonderfully dynamic pattern.

Overall, there is an interplay between horizontal and vertical striping in the body. Horizontal striping is stronger in the rear of the animal and in its lower legs, while vertical striping dominates in the front part of the torso, neck, and head. In the middle of the body the striping pattern changes abruptly, and yet there is no break. In front of and above

Figure 1 (above). Plains zebras in the Moremi Game Reserve, Botswana. (Photo: C. Holdrege.)

Figure 2. Two plains zebras in the Ngorongoro Crater, Tanzania. (Photo: David Dennis; Wikimedia Commons.)

the rear legs, the wide stripes begin on the belly in vertical orientation, then curve toward the horizontal on the rump. As they approach the animal's rear end, each of the black stripes narrows to a tip so that the rear end is more white than black. On the rump the horizontal stripes are broad and become narrower on the legs. The lower part of the legs can also have horizontal stripes, which are very narrow. The horizontal striping at the rear covers the rump and the strong leg and pelvic muscles that thrust the animal forward when it moves.

In contrast, the front legs carry most of the body's weight, and the horizontal leg stripes arch upward into the vertical stripes of the shoulder and neck, continuing into the upright standing hair of the mane. It's worth attending to how the "flow" of the horizontal leg stripes morphs into the vertical stripes of the shoulders. These two "streams" meet right at the anatomical elbow (which looks like the shoulder) and form a series of upward arching triangular shapes. All this emphasizes the gesture of upward movement.

Each individual animal can be identified by its own unique striping pattern—a whole-body "fingerprint" displayed to the world. When looking closely, you can see the variation in stripes on the flanks of the animals (Figures 3 and 6). A particularly striking example of individual differences can be seen in the photos of the heads of four different zebras in Namibia. Such examples show us that we need to be cognizant of the many variations on a theme that occur.

Figure 3. Plains zebras in the Lake Nakuru National Park, Kenya. (Photo: Daryona; Wikimedia Commons.)

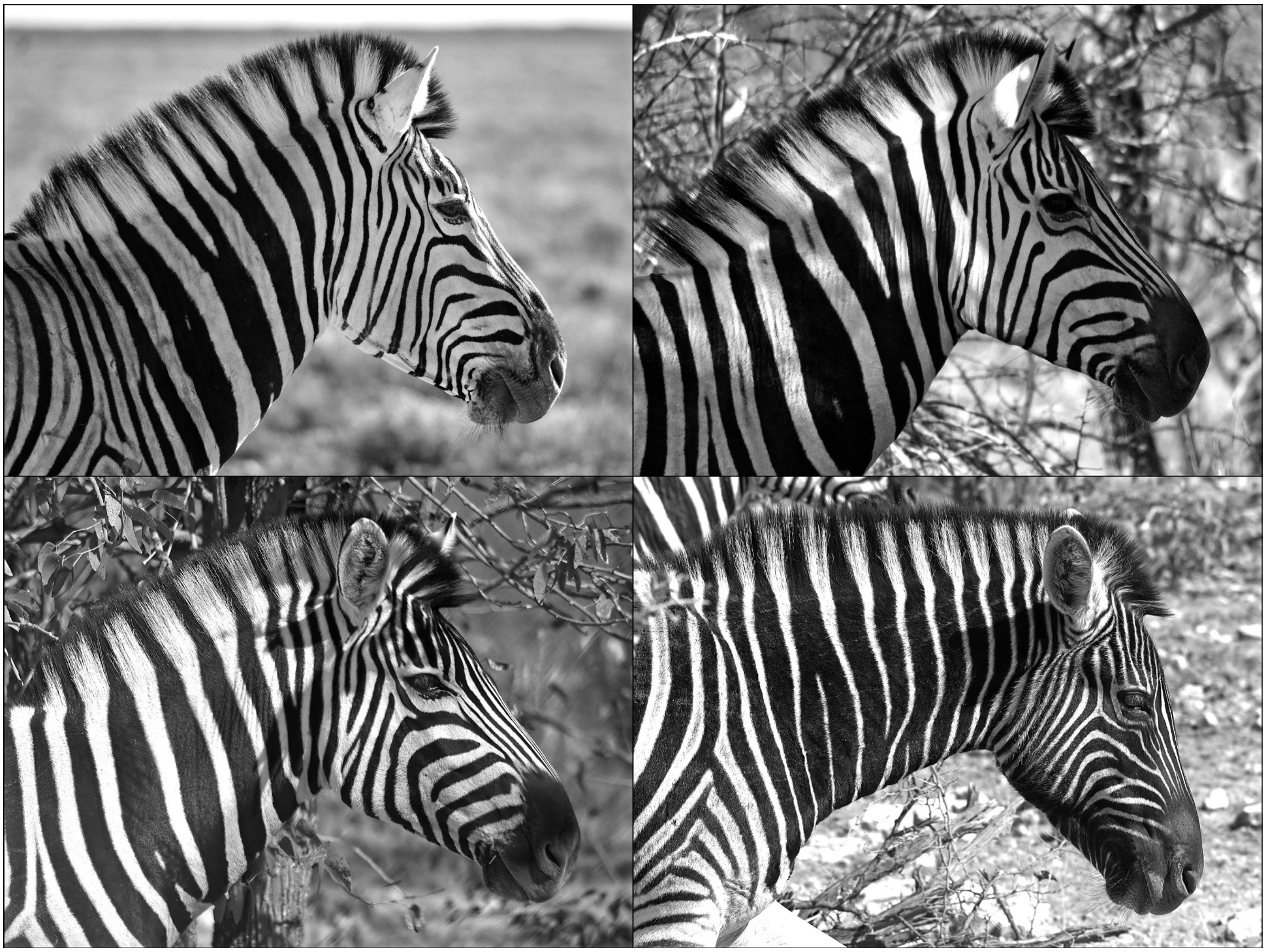

Figure 4. Variation in the stripe pattern in four different individual plains zebras; Etosha National Park, Namibia (Photo: Hans Hillewaert; Wikimedia Commons.)

All in all, the rhythmical striping pattern is a harmonious and dynamic whole in which each band relates to its neighbor. Moreover, in the individual variations we witness a kind of creative playfulness of nature that creates sameness (pattern) which is never the same.

"Presentation Value"

Twentieth-century Swiss zoologist Adolf Portmann pointed out that in many closely related species there is more generic sameness in the hidden inner organs and greater species specificity in the external visual appearance (Portmann 1967). No one would confuse a zebra and a horse based on outer appearance, and of course, they inhabit different environments. They belong, together with asses, in the genus *Equus* and their internal organs, skeleton, and muscles are remarkably similar. Only a specialist can tell them apart. Similarly, the lion's skeletal and muscle structure are very similar to the tiger's (both are in the genus *Panthera*), but no one would mistake the striped tiger for a lion.

Portmann coined the term "presentation value" (*Darstellungswert*) to point to the significant attention nature has given to external appearances—how animals present themselves to the world through color, shape, pattern, sound, smell, or texture (1967, Chapter XI). Portmann wants us to take the appearances of nature seriously, and not to assume they are simply fortuitous results of organic development that "just happen." When we do take appearances such as zebra stripes seriously, our awe of nature's creativity grows and at the same time, as Portmann puts it, we are led to a "vista of the inexpressible." In other words, we are confronted with the riddle of what nature is expressing through outer patterns such as zebra stripes. We can try to find connections and relations by comparing patterns, say, in different groups of animals, as Portmann did, and more recently biologists such as Wolfgang Schad (2012) and Mark Riegner (1998).

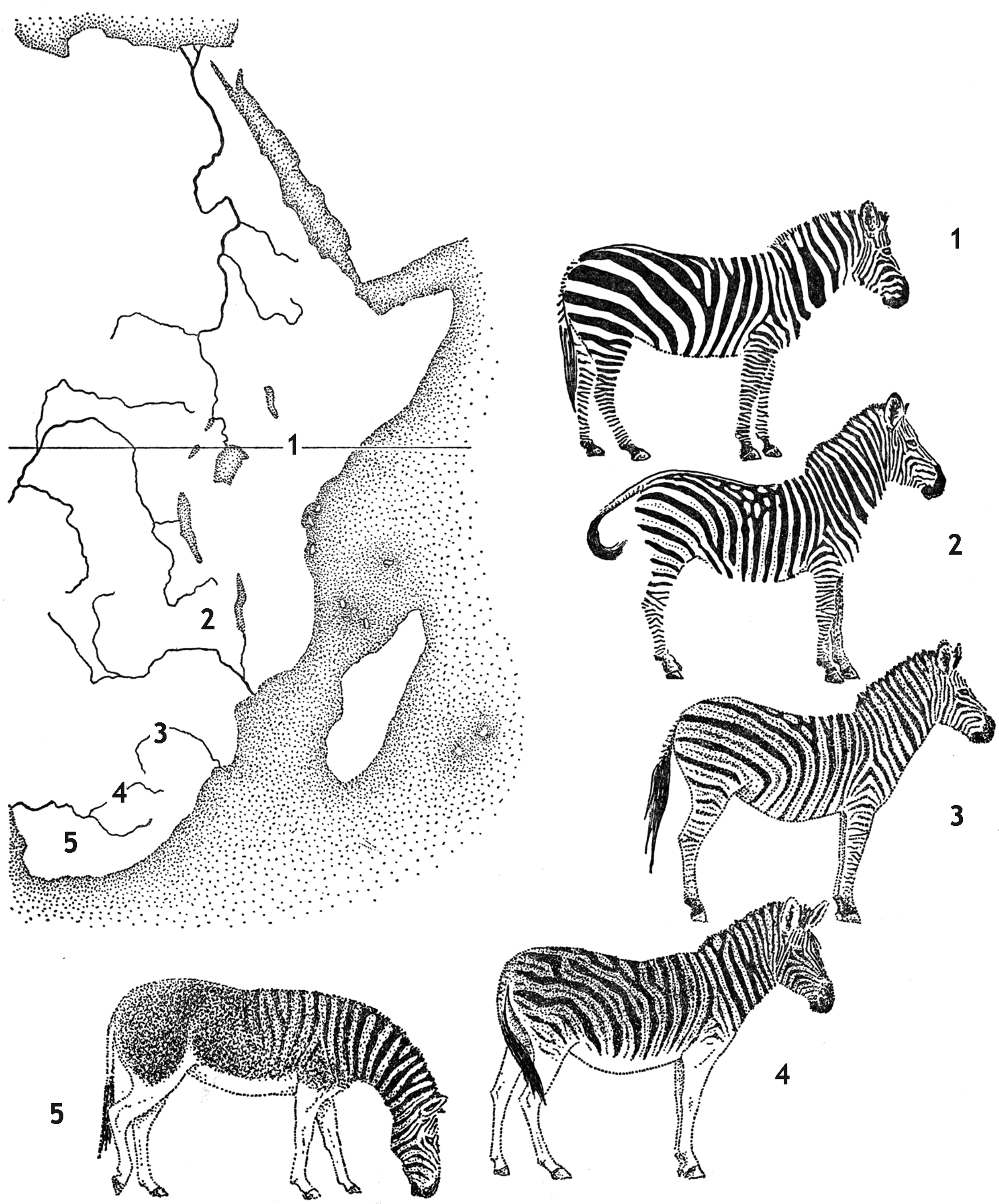

Figure 5. Examples of the geographical variation in stripe pattern in the plains zebra (*Equus quagga*). (1) Grant's zebra (*E. q. boehmi*). (2) Selous' zebra (*E. q. selousi*). (3) Chapman's zebra (*E. q. chapmani*). (4) Burchell's zebra (*E. q. burchellii*; extinct). (5) Quagga (*E. q. quagga*). See text for further explanation. (Drawings by Andreas Suchantke; from Suchantke 2001, Figure 4, p. 8; figure altered and simplified by C. Holdrege.)

In the case of zebras, it has long been noticed that there is geographic variation in the striping patterns of the different subspecies and populations of plains zebras (Cabrera 1936; Suchantke 2001; see Figure 5). Generally speaking, in the equatorial region the contrast between the black and white bands is most pronounced, and the stripes extend all the way down the legs (Figure 5, #1). Further south, many individuals have lighter stripes between the black and white bands; they are called shadow stripes (#3).

Then there are two extinct subspecies of the plains zebra that lived in South Africa. Burchell's zebra (*Equus quagga burchellii* was more reddish than black, the stripes were not as defined, especially toward the rear of the animal, and they did not extend down the legs (#4). Finally, the Quagga

Figure 6. Nursing plains zebra foal during the dry season; Moremi Game Reserve, Botswana. (Photo: C. Holdrege.)

(*Equus quagga quagga*) had stripes only in the front half of the body and had no leg stripes (#5).

Of course, within any given population there is, as I mentioned, considerable variation, so the geographical differences are not clear cut. Biologist Andreas Suchantke noted that on the equator the difference between bright light and shade is stronger than in all other latitudes, given the high daily arc of the sun's path each day. He suggested that the zebra's coat pattern variation in a way parallels changing light relations from equator to the subtropics, with the shadow-light contrast becoming weaker further away from the equator. So the changing pattern expresses in a surprising way a relation to the changing light environment, without the connection being in any narrow sense adaptive or utilitarian. It's an intriguing idea. But what gives me pause, as Ruxton (2002) points out, is that the mountain zebra (*Equus zebra*) is strongly striped and lives in South Africa far from the equator, inhabiting areas that formerly the only partially striped Quagga also inhabited.

"What Are Stripes Good For?"

Most professional biologists who have concerned themselves with zebra stripes have asked a narrow question: what are zebra stripes good for? In other words, they "make the implicit assumption," as the authors of a recent article about zebra stripes stated, that the stripes are adaptive (Larison et al. 2015). "Adaptive" means that they must now have, or must once have had, a specific function that contributed to the survival of the animal. All "appearances," on this view, exist because over time they arose fortuitously through changes in genetic and developmental mechanisms, but were useful to the animal so that they were perpetuated through the generations. This is the standard thought form—the conceptual lens—through which biologists today attempt to account for any and all appearances.

The result has been a plethora of stories (often called hypotheses)—at least 18 different ones—to account for zebra stripes (Ruxton 2002, Larison et al. 2015, Caro et al. 2015; Caro 2016). They provide camouflage in tall grass or in poor light conditions; they make zebras look bigger than they are so as to confuse attacking predators; they reinforce social bonding; they help with regulating body temperature; they protect against biting flies such as horse flies or tetse flies. The list goes on.

In the past couple of decades, some biologists have looked more carefully at these suggested explanations of zebra stripes (Ruxton 2002, Larison et al. 2015, Caro et al. 2015; Caro 2016). They looked at the evidence on which the conjectures were based. In some cases there are anecdotal observations that support the idea of an adaptive function of stripes in specific situations. But more often than not the stories about why zebras have stripes turn out to reflect, not any compelling evidence, but rather the researchers' need for some functional explanation.

Tim Caro, a professor of wildlife biology at the University of California, Davis, has done the most thorough examination of "explanations" of stripes. To take one example, he says that "biologists have long remarked on the resemblance between the repeated pattern of stripes on zebras

Figure 7. Two plains zebras grazing during the dry season; Moremi Game Reserve, Botswana. (Photo: C. Holdrege.)

and the vegetation of the habitats in which they live" (2016, p. 23). In tall growing grass there can be vertical bands of illumination and darkness. And in the early morning and late afternoon there are particularly vivid shafts of shadows contrasting with the brighter vegetation. Some observers have noted in such appearances a certain resemblance to the vertical stripes in the front part of the zebra's torso. Or when a zebra is in woodlands, its pattern can, to a degree, mimic shadow-brightness patterns, and also the darker trunks and horizontal branches of trees that are separated by bands of brightness.

Clearly, such observations of what we might call an "agreement of appearances" can be noted in certain specific conditions as fleeting phenomena. But the agreement (camouflage) is even then very approximate (Melin et al. 2016). The zebra does not live in a black-and-white striped world into which it disappears. And during moonless nights all animals blend equally with the darkness and, from a visual point of view, are well camouflaged—yet it is on moonless nights that zebras most often fall prey to lions (Elliott et al. 1977; Funston et al. 2001).

On the whole, zebras are visually highly conspicuous during the day time, whether in open grasslands or in woodlands. Moreover, "compared to many hoofed animals on the plains of Africa, they are remarkably mobile and noisy and never attempt to hide in cover" (Morris, cited in Ruxton 2002, p. 238a). Nonetheless, another popular "explanatory" story is that the striping pattern, especially when zebras are moving and in groups, could in a variety of ways confuse predators. But lions attack and successfully kill zebras whether they are solitary or in groups, and as just mentioned, most kills are at night when stripes could not dazzle or confuse lions. Again, it may be the case that once in a while, in a particular context, the striping pattern confuses an attacking lion for a moment and the zebra escapes. But it is not a pronounced tendency.

Caro performed many field experiments to test the hypotheses about stripes, and discusses these along with a plethora of other researches in his 2016 book *Zebra Stripes*. The careful research summarized in the book leads him to reject virtually every hypothesis. What he doesn't do is to question whether a survival-based explanation exists. He is not moved to drop his conceptual lens.

His own conclusion is that stripes are "an evolutionary response to pressure from biting flies" such as tsetse flies, or from horse flies that belong to the Tabinid fly family (Caro 2016, p. 193). Such flies can transmit diseases and cause substantial bleeding in the many large mammals they bite. One supporting observation is that, in field experiments, some of these flies tend to avoid black-and-white-striped surfaces. Caro and his colleagues believe there is a correlation between biting fly abundance and the degree of striping among zebras and other members of the horse family (asses, horses). He marshals a number of additional observations and thought connections that he thinks support this hypothesis. In a 2014 journal article, he and his colleagues concluded that "a solution to the riddle of zebra stripes, discussed by Wallace and Darwin, is at hand" (Caro et al. 2014).

Another group of researchers, led by Brenda Larison at UCLA, disagreed (Larison et al. 2015a, 2015b). They pointed out that biting fly abundance was not directly observed, and there was a lack of data about abundance and distribution. What Caro and colleagues did was to use two environmental conditions—temperature and humidity—as proxies to estimate the abundance of biting flies, which tend to be more prevalent in warm, humid conditions. As a result, "what they [Caro et al.] call 'tabanid distribution' could easily correlate with any number of species distributions, be they insects, plants, or vertebrates." In their own research on plains zebras, Larison and colleagues found variation in striping pattern to be most strongly correlated with temperature. What that correlation means, and whether—as Larison and colleagues assume—it has to do with an adaptive function, remains open.

Let's assume, for the sake of argument, that research continues and researchers were to find that there is a correlation between stronger striping in zebras in areas with greater abundance of biting flies. And let's assume, in addition, that widespread field observations of zebra populations reveal that horse flies are less likely to bother boldly striped zebras than others. Would we, with this additional evidence, have explained or accounted for zebra stripes? Would we have a "solution to the riddle of zebra stripes?" Would we know why zebras have stripes? Of course not.

What we would know is that stripes play a role in defense against horse flies, just as they may under certain conditions provide camouflage, or make zebras stand out more. But all of these "functions" could have arisen as propitious side effects of the striping pattern.

Moreover, in such purported "explanations," the pattern in its concreteness, in all its nuances and variations, is glossed over because one only focuses on the abstraction: black and white (or dark and light) surfaces that are clearly distinguishable. These could be blocks, circles, blotches, straight bands, etc., so the explanation would not tell us why zebras specifically have *stripes*. The explanation is detached from the real animal.

I do not have an explanation for the zebra's stripes. I am not looking for an explanation. I'm trying to get closer to what the animal may reveal as its unique way of being. By attending to the stripes I've been led to see an expression of nature's creative power and am intrigued by each new variation. The zebra's wonderful stripes remain a riddle for me. I'm happy to wait and see whether further insights arise.

References:

Cabrera, A. (1936). "Subspecific and Individual Variation in the Burchell Zebras," *Journal of Mammalogy* vol. 17(2), pp. 89-112. doi: 10.2307/1374181

Caro, T. et al. (2014). "The Function of Zebra Stripes," *Nature Communications* vol. 5, pp. 1-10. doi: 10.1038/ncomms4535

Caro, T. and T. Stankowich. (2015). "Concordance on Zebra Stripes: A Comment on Larison et al. (2015)," *Royal Society Open Science* vol. 2. doi: 10.1098/rsos.150323

Caro, T. (2016). *Zebra Stripes.* Chicago: University of Chicago Press.

Elliott, J. P. et al. (1977). "Prey Capture by the African Lion," *Canadian Journal of Zoology* vol. 55(11), pp. 1811-28. doi: 10.1139/z77-235

Funston, P. J. et al. (2001). "Factors Affecting the Hunting Success of Male and Female Lions in the Kruger National Park," *Journal of Zoology* vol. 253, pp. 419-31. doi: 10.1017/S0952836901000395

Larison, B. et al. (2015a). "How the Zebra Got its Stripes: A Problem with Too Many Solutions," *Royal Society Open Science* vol. 2. doi: 10.1098/rsos.140452

Larison, B. et al. (2015b). "Concordance on Zebra Stripes is not Black and White: Response to Comment by Caro & Stankowich (2015)," *Royal Society Open Science* vol. 2. doi: 10.1098/rsos.150359

Melin, A. D. et al. (2016). "Zebra Stripes through the Eyes of Their Predators, Zebras, and Humans," *PLOS ONE* vol. 11(3). doi: 10.1371/journal.pone.0151660

Portmann, A. (1967). *Animal Forms and Patterns*. New York: Schocken.

Riegner, M. (1998). "Horns, Hooves, Spots, and Stripes: Form and Pattern in Mammals." In Seamon, D. and A. Zajonc (editors), *Goethe's Way of* Science. Albany, NY: SUNY Press.

Ruxton, G. D. (2002). "The Possible Fitness Benefits of Striped Coat Coloration for Zebra," *Mammal Review* vol. 32, pp. 237-44. doi: 10.1046/j.1365-2907.2002.00108.x

Schad, W. (2012). *Säugetier und Mensch* (2 volumes). Stuttgart: Verlag Freies Geistesleben. (A translation of this book is in progress; a translation of the first edition of the book exists: *Man and Mammal,* Garden City, NY: Waldorf Press, 1977.)

Suchantke, A. (2001). *Eco-Geography*. Great Barrington, MA: Lindisfarne Books.