SACRED BOVINES

HOW THE TIGER CHANGED ITS STRIPES

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"You can't expect a tiger to change its stripes." Or so the adage goes. Nor, apparently, can a leopard change its spots. Even the writers of the Bible said so, centuries ago (Jeremiah 13:23). Namely, people widely believe that every species has its own special "nature." This immutable essence is supposed to guide how the organism functions. Indeed, an organism that does not fully express its "inner nature" is considered by many as somehow unhealthy or incomplete. Only negative consequences can ensue (Griffiths, 2002, p. 79). Biologists observe otherwise, of course. Yet this intuition – call it *species essentialism* (this month's Sacred Bovine) – is widespread and can persist even after evolution education. It is deeply rooted in our intuitive teleology (Keleman & Rosset, 2009). Yet a few fascinating – and sometimes playful – cases of color patterns in animals might prompt reflection, questioning, and learning.

○ What Makes a Tiger a "Tiger"

The belief that a tiger's stripes or a leopard's spots are essential is based foremost on a view that they exhibit an intended purpose. In this case, the predator "must" be inconspicuous to prey. That seemed clear even to Rudyard Kipling (no biologist himself), who described it in one of his now classic *Just So Stories*, "How the Leopard Got His Spots." The Leopard character moves from the fields to the jungle, which is all "speckled and sprottled and spottled, dotted and splashed and slashed and hatched and cross-hatched with shadows." A bystander observes his new spots and notes: "You can lie out on a leafy branch and look like sunshine sifting through the leaves; and you can lie right across the centre of a path and look like nothing in particular. Think of that and purr!" (Kipling, 1912, p. 59). That is, the leopard's spots – as much as the tiger's stripes – fulfill a "necessary" function.

All the traits of a tiger apparently contribute to its "nature." For amusement, imagine a tiger munching a tasty salad: a vegetarian tiger?! No, the claws, the huge canine teeth, the roar, the stalking, the padded paws all seem to speak to its imagined "natural purpose" of hunting animals.

Essentialism is based, first, on perceived purpose, but also involves two other concepts: universality and fixity. Namely, *all* tigers have stripes. And, as the adage indicates, they cannot change. They are innate. Nowadays, that is viewed in terms of genetic determinism. Purpose, universality, and fixity: together these features foster essentialist views. Biologists, of course, know better. The essentialist view is nowhere *justified*. Rather, it emerges from psychological tendencies. So, to address the deep preconceptions, one needs startling images to provoke awareness and reflection.

Ironically, essentialism fits comfortably with the evolutionary notions of adaptation and genetic "blueprints." So the strategy here is to focus on developmental factors and variation at the population level.

○ Do All Tigers Have Stripes?

Under intuitive thinking, the tiger's stripes are essential, so all tigers must have them. Or else they fail to be "true" tigers.

So, what should one say about a stripeless tiger (Figures 1 and 2)? These are not just white tigers with stripes (which are also found). Nor are they albinos. These are tigers without stripes. One lounges comfortably with her siblings, who exhibit the more common pattern. That

Figure 1. Not all tigers have stripes. Here, a stripeless tiger sits with her two siblings (photo courtesy of Cango Wildlife Ranch).

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Figure 2. Stripeless tigers are not common, but they are not wholly uncommon (photo by Krzysztof Duda, YouTube).

Figure 5. Not all cheetahs are fully spotted. Here, a "king cheetah" with stripes crouches next to one with the more common pattern (photo by Greg Barsh, courtesy of Ann van Dyke Cheetah Centre).

Figure 3. Not all zebras are uniformly striped. Some have spots (photo via Bonnie Cook, Pinterest).

is, the other tigers seem to regard her as a member of the species. Not an error. Just one of the family. Why should we reject their judgment?

Consider, next, other remarkable variants. What about a zebra that has spots, rather than stripes (Figure 3)? These are not so uncommon, either. One mare in Botswana gave birth to three such zebras from 2005 to 2009. Again, should we conclude that these are not true, full-fledged zebras?

Other zebras lose some of their stripes entirely. In these cases, they do not lose their black stripes to become white. Rather, developmentally, zebras form white stripes on a dark background (Prothero & Schoch, 2003). So, without the white stripes, patches appear dark again, as in their ancestors (Figure 4).

Given these examples, one might wonder if it is possible for a wild cat to change its proverbial spots? Apparently so. Some cheetahs, known as "king cheetahs," have *stripes* instead of spots (Figure 5)!

All these unexpected cases help erode the intuitive belief in universality. It is easy, of course, to dismiss the exceptions as "abnormal" or "deviant": less than an imagined ideal. But one can easily see that such labels are value judgments, not neutral descriptive science (see Sacred Bovines, November 2007). All these animals appeared in nature. Hence, they cannot be "unnatural." Stripes (or spots) are plainly not necessary, even if they are predominant. The lack of universality here helps expose the faulty essentialist assumption.

Figure 4. Some zebras have lost their stripes. Here, a pseudomelanistic zebra grazes next to a striped kin (photo courtesy of Linda De Volder).

○ Transforming Tiger Stripes

That still leaves the essentialist notion of fixity, or immutability. But the variation among tigers, zebras, and leopards from one generation to the next also

Figure 6. Stripes can sometimes change from one generation to the next. Here, a pseudomelanistic zebra foal stands next to her mother (photo by Michael Fitt, courtesy of Wilderness Safaris).

Figure 7. White stripes on the African striped mouse appear where melanocytes have been switched off by the interaction of diffusing morphogens (photo by J. F. Broekhuis).

embodies change. The "anomalous" examples above were all born to "normal" parents (Figures 1 and 6). Something happened.

We now have good biological understanding of how stripes and spots develop, and thus of how slight variations can yield changes. In the 1950s, mathematician Alan Turing described how morphological causal factors diffusing across an area between two source points could interact to create banding patterns. They resemble the interference patterns created in wave tanks in physics classes (Murray, 1988). Turing's scheme certainly works with chemicals in nonliving media (Jones, 2016). Now the patterns have been documented in zebrafish (Nakamasu et al., 2009) and lizards (Edelstein-Keshet, 2017). Indeed, the same mechanism helps create

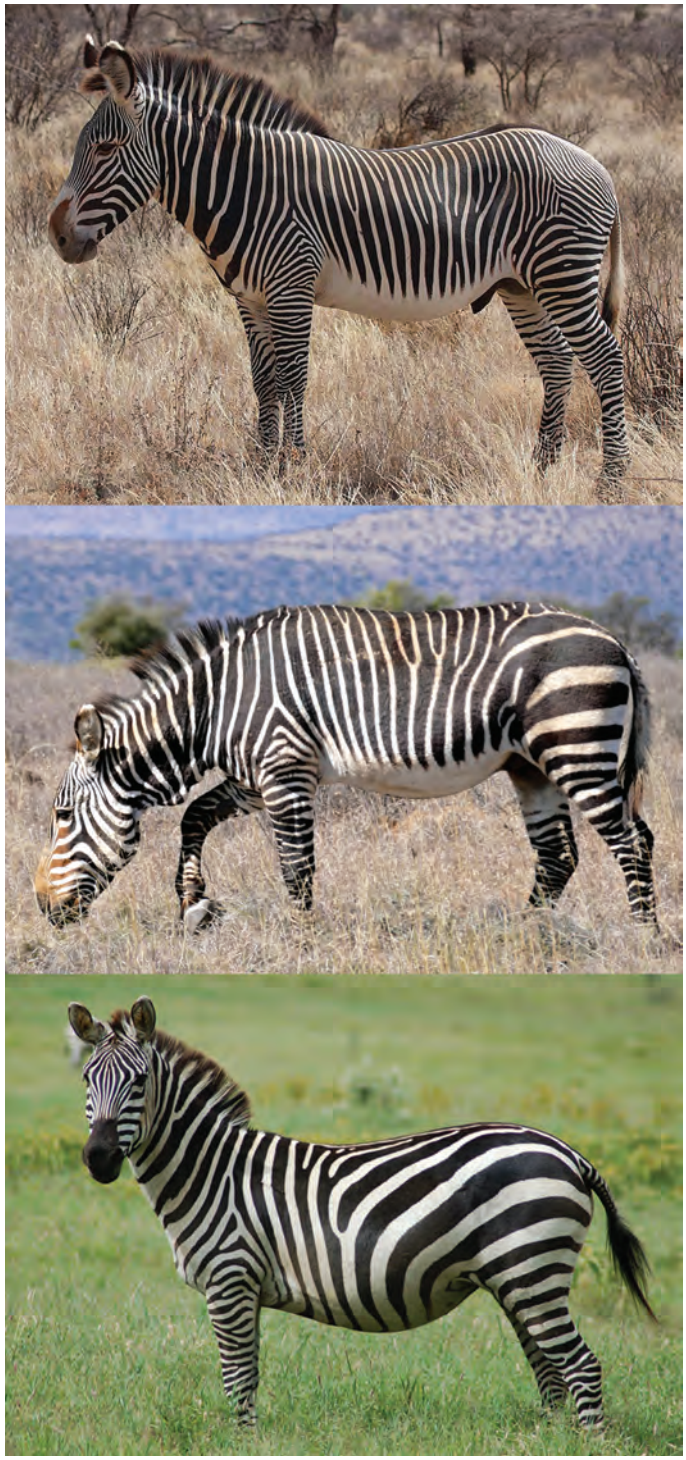

Figure 8. Zebra stripes vary in number and width based on when they begin developing in the embryo (from the top, photos by Rainbirder; Bernard Dupont; Joachim Huber, cc2 Wikimedia).

the human hand and foot. The cells in the "stripe" die, leaving space between the phalanges: hence, separate fingers and toes (Sheth et al., 2012). The process also leads to the ridges of the palate in the mouth (Economou et al., 2012).

Recently, the Turing patterns have been linked to pigmentation in specific cells. In the African striped mouse (and chipmunks, too), the

Figure 9. Our hands are striped. Polydactyly reflects a change in the underlying Turing pattern, based on timing in development (Wikimedia).

Figure 10. The transition from "mackerel" to "blotched" tabby cat is governed by one transmembrane protein (potos by Hirashi and Cassie J., cc2 Wikimedia).

Figure 11. A melanistic leopard (or "black panther") shows its spots in infrared imaging (photo courtesy of Laurie Hedges).

Figure 12. A spotless cheetah, like a black panther, shows pigmentation effects that eclipse underlying patterns (photo by Guy Combes).

white stripes along the midline of the back form by switching off pigment production in the band's melanocytes (Figure 7) (Mallarino et al., 2016; Yong, 2016).

To change these patterns, all one need do is tweak one of the variables: the rate of the diffusion, the amount diffused, the initial timing, the response of the cells to particular concentrations of the diffusing signals. They can change the complexity, the size, the direction, or the regularity of coloration patterns (Allen et al., 2011). For example, if one changes the time when the pattern begins to form, zebras (from different species) develop different numbers of stripes, with different widths (Figure 8) (Bard, 1977). In the same way, human hands can develop more bands, and hence more digits: polydactyly (Figure 9).

Recent research shows that in domestic cats, a single factor governs the transition between two tabby patterns: "mackerel" (striped) and "blotched" (Figure 10) (Eizirik et al., 2010). That same factor also transforms a cheetah into a "king cheetah" – once viewed as so different that it was construed as a separate species entirely (Figure 5)! The key element in this case is a transmembrane protein

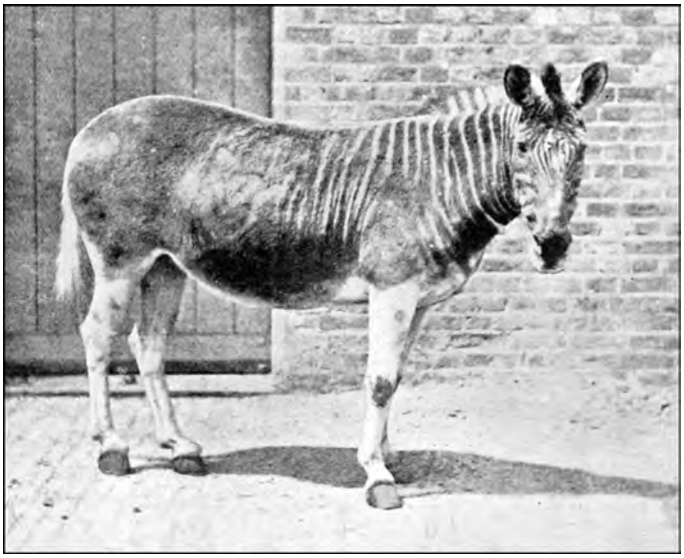

Figure 13. One of the last quaggas in 1870, its coloration reflecting its divergence from other zebra types (see Figure 8) (Wikimedia).

(aminopeptidase Q), which likely responds to chemical signals from nearby cells (Kaelin et al., 2012). Apparently, then, tigers *can* change their stripes.

Other factors can affect overall pigmentation: yet another way to change one's spots or stripes. Black panthers are really leopards in disguise. Melanocytes active over the entire surface eclipse the underlying rosette pattern. Using infrared light, however, one can still detect the spots (Figure 11) (Hedges et al., 2015). Here, we notably encounter a vestige of the past, which helps to document the change that occurred. One can also lose an "essential" pattern through loss of relevant pigments, as in the spotless cheetah (Figure 12).

Of course, it is easy to imagine how morphogens or developmental factors may be genetically based. Proteins that help regulate cell processes will be encoded by genes. And those genes may mutate. Further, a mutational change in the germ line may be passed on to the next generation. When that happens, a pattern variant (even if rare) may well be shared by different offspring of the same parent(s), as in the cases noted above. Recently, the tabby pattern factor in felids (mentioned above) has been mapped to the gene *Taqpep*. A second gene contributes to the coloration by responding to the underlying Turing patterns (Kaelin et al., 2012). In another case, in mice the *Mitf* gene is responsible for development of melanocytes, but it can be suppressed by *Alx3*. Both are implicated in the white stripes of chipmunks (Mallarino et al., 2016; Yong, 2016).

Once such mutations emerge, their developmental consequences can cascade through succeeding generations, changing the lineage: hence, evolution. That would surely explain the similarities and differences in striping among the various zebra types in Africa (Figure 8), along with the now extinct quagga (Figure 13): they all reflect pattern changes from some common ancestor (Leonard, 2005; Larison, 2012). Ultimately, the "essential" features of a species – epitomized by the tiger's stripes – are open to developmental change, possibly for the long term.

○ Essentialism & the Irony of Change

What is a species' "essence"? Ironically, while the image of a tiger's essence seems to be its unchangeable stripes, the imagined essence of a chameleon is quite the opposite: namely, its ability to change its color. Other organisms, too, change their color or appearance in short-term physiological or behavioral responses: squid and cuttlefish, flounders, cichlids, wrasse, anolis lizards, and the golden tortoise beetle, among others. Indeed, responses to changes in the environment seem commonplace. Some of those changes may be short term, some long term. Behavior, development, cellular processes, ecology, and inheritance all interact. So that raises the question again of why we might expect to find immutable essences among living things.

Yes, a tiger *can* change its stripes. Zebras, too. And zebrafish. And cats and mice and chipmunks. And human hands, in a sense. Likewise, leopards can change their spots. Along with cheetahs. The ultimate question may be instead: Can human assumptions about essentialism also change, through learning?

Note: All images are available electronically at http://sacredbovines.net/tigerstripes.

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