

Reply to Bar-Oz and Lev-Yadun: Horse colors in time and space

The wide variation of fur and plumage colors in animals has fascinated people throughout history, and biologists have long debated its prominent role in evolution. Notably, Charles Darwin emphasized the importance of this phenotypic trait in his *On the Origin of Species* (first published 1859). However, although the importance of coat color in adaptation has been well documented, the underlying genetic mechanisms are less well understood.

The results of our studies on Paleolithic horses (1, 2) suggest that color phenotype variation in predomestic horses was greater than commonly assumed. We agree with Bar-Oz and Lev-Yadun (3) that the observed phenotypes mostly likely reflect the selection pressures imposed on horse populations by surrounding habitats. Evidence for this conclusion was produced in recent studies of mainland and beach mice from Florida (4) and of reintroduced wolves from the Yellowstone National Park (5), showing that lighter-colored phenotypes have an adaptive advantage in open landscapes, whereas dark phenotypes are better adapted to habitats with higher vegetation cover. In agreement with the fact that Late Glacial and Holocene horses in Western Europe featured hooves best adapted to the soft substrates of forests, black horses only appear in our sample set during the Holocene (1, 2), when forest cover had substantially increased across Europe. However, our set of samples is currently too patchy to draw any firm conclusions about a possible correlation between horse phenotypes and the surrounding environment at a certain time. Therefore, we agree with Bar-Oz and Lev-Yadun that coat color variation is “not a random phenomenon but rather the outcome of selection” and that our results “highlight the sharp observation capability of Paleolithic people to document wild animals.” Additional data will

be necessary to correlate color phenotypes with the surrounding environment; for example, isotope analyses would help to elucidate the paleoenvironment and paleodiet of these animals (6). The major conclusion of our article was succinctly expressed by T.O. in the *New York Times* last year: “One of the things that most pleases me about this paper as a piece of ancient DNA science is, it kind of begins with a question. These spotty horses: were they magical or real?” Our data show they were real.

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The authors declare no conflict of interest.

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