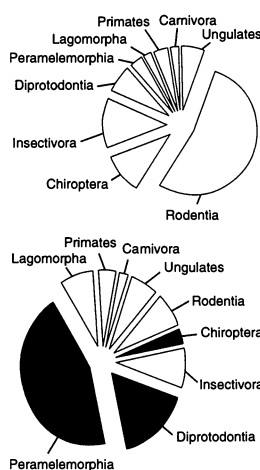


the number of species extinctions should convey differences in the relative vulnerability of these groups, because not all clades are equally speciose (the aforementioned orders comprise 43.7%, 20.0%, and 9.2% of all mammals, respectively). Given the average mammalian extinction frequency of 0.02, rodents, bats, and insectivores have not suffered more species-level extinctions than expected under a binomial distribution [using a one-tailed test and data from (2)]. In fact, the bat extinction rate is significantly lower than expected ($P = 0.02$; see the figure).

We agree that the number of ungulate extinctions is not more than expected from random ($P = 0.49$), but we emphasize that the relative vulnerability of ungulates depends on the data source used, illustrating the difficulty of describing patterns of extinction across taxa. Seven ungulate species are listed as extinct in the latest IUCN Red List (5), plus three additional species if ungulates that are extinct in the wild are counted. On the basis



Looking at extinction numbers. Differences in species-level extinctions in the last 500 years for nine mammalian orders for (top) absolute numbers of extinctions and (bottom) number of extinctions as a proportion of clade size. Red and green represent clades that have suffered more or less extinction, respectively, than expected [extinction data from (2) and clade sizes from (8) used].

of these data, ungulates have suffered more extinctions than expected ($P = 0.02$). There are only two species in common in the different data sets; indeed, four species on the IUCN Red List were disqualified by MacPhee and Flemming (2), either because of evidence that those species are extant or systematic uncertainty. In addition, over the past century a factor has arisen that might for the first time strongly select against extinction of large vertebrates: conservation. Without extensive conservation efforts in North America, for example, current ungulate diversity would likely be far poorer, missing the likes of bison, bighorn sheep, musk ox, and pronghorn [see also (4)]. How should these near misses be considered when assessing extinction risk?

Patterns will only tell us so much; sooner rather than later, we must focus on threat processes resulting in vulnerability today (1). Indeed, to complement the study by Berger *et al.* (6) that we discussed in our Perspective, we

described how carnivore reintroductions could be devastating for naïve prey populations when predators have been absent. Our view is not, however, that naïveté alone is the sole threat, but rather that “biological and anthropogenic forces” [emphasis added (3, p. 998)] critically influence taxonomic differences in extinction risk and that “extinction results from a series of factors, interactions among factors, and the multiplicative effects of these interactions.” Across mammals, it is likely that ungulates had and do have increased extinction vulnerability. Ungulates have shown a consistently high extinction vulnerability over time, despite the fact that extinction-driving processes may have altered substantially: for example, 28 out of 68 (41.2%) extinctions in the Pleistocene (2) were ungulates, and orders within the broadest definition of Ungulata (Artiodactyla, Perissodactyla, and Sirenia) are currently significantly more threatened than expected [on the basis of data from (5)].

JOHN L. GITTLEMAN,¹* MATTHEW E. GOMPPER, 2
KATE E. JONES¹

¹Department of Biology, University of Virginia, Charlottesville, VA 22904, USA. ²Center for Environmental Research and Conservation, Columbia University, New York, NY 10027, USA

*To whom correspondence should be addressed.
E-mail: jlgittleman@virginia.edu

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Tales from the DNA of Domestic Horses

IN OUR STUDY OF THE ORIGINS OF DOMESTIC horses, published in 1998, my colleagues and I examined sequence data of the mitochondrial DNA control region from 29 individuals, including Przewalski's horse and 14 domestic breeds (1). We found virtual genetic constancy within Przewalski's horse, unsurprising considering its severe historical bottlenecking, but a great deal of variation within and among domestic breeds. We wrote, “Overall, the amount of sequence divergence among modern breeds is greater than could have arisen within any plausible

timescale of domestication (approximately 5,000 years by current archaeological estimates), and clearly reflects more ancient haplotype diversity.” We concluded, “The extent of modern haplotype diversity probably reflects an input of wild animals from different areas. It is unlikely that all domestic horses sprang from a single, local population. Domestic horses arose from wild stock distributed over a moderately extensive geographical region, large enough to have contained within it considerable pre-existing haplotype diversity.”

Carles Vilà and co-authors undertook a similar analysis, incorporating some of our data, and drew essentially the same conclusions (Reports, “Widespread origins of domestic horse lineages,” 19 Jan., p. 474). Their principal finding, the widespread origins of domestic horse lineages, echoes our 1998 results, although the latter are not cited in their report. Vilà *et al.* augmented their modern mitochondrial DNA study with additional results on ancient specimens and microsatellite DNA sequences, which we did not perform and which allow them to draw some interesting subsidiary conclusions.

Although the diverse genetic input to modern domestic horses, which implies a broad geographic catchment, is suggestive of multiple domestication events in different areas, other explanations are possible—for example, that horses taken from a wide area were domesticated in one or a few places only. This is an archaeological question requiring primarily archaeological evidence, although it could be aided by the extraction, thus far unsuccessful (1), of ancient DNA from the putative centers of domestication.

ADRIAN M. LISTER

Biology Department, University College London, Gower Street, London WC1E 6BT, UK. E-mail: a.lister@ucl.ac.uk

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Response

WE SEQUENCED PART OF THE MITOCHONDRIAL DNA control region of 191 domestic horses from 10 breeds (1). Additionally, we did a complete search in GenBank, a public database for DNA sequences, which added 37 of 70 unique sequences from modern horses to our analyses [see Fig. 1B in (1)]. These GenBank sequences were referred to by their accession numbers, and eight of them were unique to the study by Lister *et al.* (2). We regret not citing this study. However, we maintain that their results were insufficient to draw firm conclusions. In their paper they said, “The modern data do not distinguish single from multi-regional domestication events, though the extent of the modern haplotype diversity probably reflects an input of wild animals from different areas” (2, p. 276). In fact,

SCIENCE'S COMPASS

Lister *et al.* perceived the work that is necessary for definitive conclusions, and it is precisely what our study has provided: "This study needs to be enlarged by accruing larger domestic samples of accurate pedigree (using both [mitochondrial DNA] and microsatellites), and by further pursuing those ancient specimens which gave indications of DNA preservation..." (2, pp. 276-277).

Moreover, the fact of high genetic diversity alone, as found by Lister *et al.* and other authors before them (3), is not sufficient to suggest a widespread origin of modern horse lineages. Large populations can have substantial genetic diversity. In this sense, sampling of a large diversity of modern horses coupled with sequences from late Pleistocene horses from Alaska that we examined is a necessary prerequisite to definitive conclusions. Our study represents the first attempt to characterize the genetic diversity in a wild horse population before domestication. The limited diversity we observed in

this ancient population suggests that multiple populations of wild horses were likely involved in the origin of domestic horses.

We agree with arguments by Lister *et al.* that archaeological discoveries are fundamental to an understanding of the domestication process. However, early domestic horses likely were indistinguishable from their wild counterparts (4); hence, the timing and location of domestication are not easily revealed by a morphologic study. DNA analysis of archaeological specimens might assist in this regard if population-specific markers could be found. However, DNA

is not readily isolated from material in areas where horses were likely first domesticated, as indicated by Lister and co-authors' inability so far to genetically characterize some of these horses. Specimens from the Arctic permafrost, where the likelihood of DNA preservation is high, or more recent archaeological sites might offer our only perspective into the genetics of ancient horses. This is the ap-



Molecular evidence from both modern and ancient wild horses is providing clues to the origins of domestic horses.

proach that we chose to take.

CARLES VILÀ,^{1*} HANS ELLEGREN,¹
ANDERS GÖTHERSTRÖM,² JENNIFER A. LEONARD,³
ROBERT K. WAYNE³

¹Department of Evolutionary Biology, Uppsala University, Norbyvägen 18D, S-75236 Uppsala, Sweden; ²Archaeological Research Laboratory, Stockholm University, S-10691 Stockholm, Sweden; ³Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, California 90095-1606, USA

*To whom correspondence should be addressed.
E-mail: carles.vila@ebc.uu.se

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