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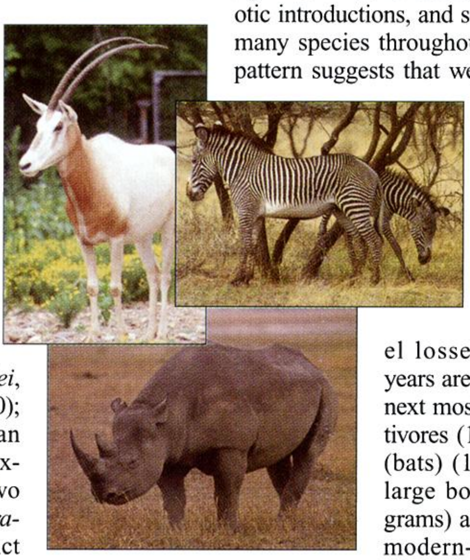
Extinction: Complexity of Assessing Risk

IN DISCUSSING THE EXTINCTION RISK OF naïve prey species confronted by reintroduced predators (*Science*'s Compass, 9 Feb., p. 997), J. L. Gittleman and M. E. Gompper say that, apparently because of diverse anthropogenic impacts, "a markedly higher proportion of ungulate species compared with other mammalian taxa have become extinct in the past 500 years."

Not so. Although the belief seems to be widespread that large mammals such as ungulates have suffered substantial losses during the modern era (that is, the last five centuries), the facts lead to a different conclusion. Of the ~90 well-corroborated extinctions that have occurred at the species level within Mammalia during the past 500 years (*1*), only five species (6%) are members of Ungulata, when the broadest available cladistic definition of this taxon is used (*2*): two Malagasy hippos (*Hippopotamus madagascariensis* and *H. lemerlei*, both extinct around 1500); a North Pacific sirenian (*Hydrodamalis gigas*, extinct by 1768); and two African bovids (*Hippotragus leucophaeus*, extinct by 1800, and *Gazella rufina*, extinct before 1894). Of these, the first three are reasonably regarded as "first contact" extinctions, although the role of human overhunting in forcing these losses is evident only in the case of the sirenian. There is no meaningful evidence regarding the cause of loss of the two African bovids (*1*).


The grevy zebra (*Equus grevyi*), Sahara oryx (*Oryx dammah*), and black rhino (*Diceros bicornis*) are listed as endangered, extinct in the wild, and critically endangered, respectively, on the IUCN Red List.

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Getting the numbers right is important because extinction (loss of all members of a minimally diagnosable evolutionary unit) is a phenomenon in its own right, although it is often treated as merely the final stage of endangerment. Rating schemes, like the IUCN Red List, that attempt to assign extinction risk factors to endangered species are, of course, extremely important as possible guides to the planet's biotic future. But history is also important, even if its lessons are slippery. For example, the nature and cause of end-Pleistocene extinctions in the continental New World, which Gittleman and Gompper cite for their probative value, are in fact still obscure. If human overhunting of behaviorally naïve species were mostly to blame for these losses [amounting to 130 species by our count (*1*)], how is it that during the past 10,000 years, there have been only two mammalian species-level extinctions (a Mexican cottontail and the sea mink) in the continental Americas—despite significant habitat destruction, numerous exotic introductions, and severe persecution of many species throughout this period? This pattern suggests that we should be looking for other factors as well in first-contact extinctions (*3*). So who has suffered most among mammals in recent times? More than 50% of all species-level losses in the past 500 years are rodents; the groups next most affected are insectivores (13%) and chiropters (bats) (10%). Mammals of large body size (>44 kilograms) account for ~12% of modern-era species losses across all taxa (*1*). In other words, modern-era mammalian losses have been overwhelmingly minifaunal rather than megafaunal. And they have been overwhelmingly insular: the world's islands have been much more severely affected by species-level extinctions in recent times than have any continental biotopes, including the world's rainforests. If these patterns continue, it is the small, the island-bound, and the least charismatic that will continue to suffer most.

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Response

ALTHOUGH EXTINCTION APPEARS SIMPLE—a species is extinct when its numbers die out—it actually is a function of biological characteristics among organisms, causal processes that influence survival, and temporal patterns during which extinction processes occur (*1*). R. MacPhee and C. Flemming illustrate this complexity by questioning our statement regarding the proportion of ungulate species that have become extinct in the past 500 years.

On the basis of their data (*2*), only 6% of the mammalian species that have gone extinct in this time period have been ungulates, in contrast to other orders that appear more extinction-prone (Rodentia, Chiroptera, Insectivora), with a combined total of 75% of all extinctions. However, as we suggested (*3*) on the basis of an original statistical test (*4*),

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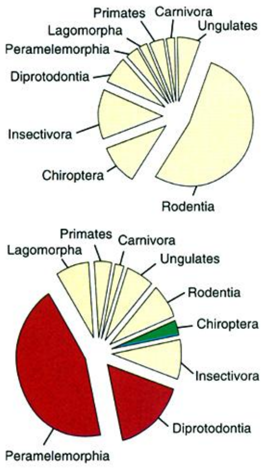
the number of species extinctions should convey differences in the relative vulnerability of these groups, because not all clades are equally speciose (the aforementioned orders comprise 43.7%, 20.0%, and 9.2% of all mammals, respectively). Given the average mammalian extinction frequency of 0.02, rodents, 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 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?



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].

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*)].

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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 preexisting 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.

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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,