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Ecology and Catastrophic Mortality in Wild Horses: Implications for Interpreting Fossil Assemblages

Abstract. *The identities, sexes, and reproductive status of groups of wild horses (*Equus caballus*) living in the Great Basin Desert of North America were known prior to their deaths on ridgelines. Another group of very young horses died on a quagmire. Snow accumulation or drought was apparently responsible for the mass deaths. These data have implications for reconstructing some aspects of the social structure of fossil mammals on the basis of skewed sex or age ratios in bone assemblages.*

Socioecological interpretation of fossil mammalian assemblages is a fairly recent field of study (*1*), although grouped remains of fossil bison, camels, pigs, rhinos, prongbucks, horses (*2*), and dinosaurs (*3*) have been used as evidence of complex social structures because of biased sex ratios or adult females situated in proximity to young. Such group remains potentially provide information about social structure of a species. Because groups varying in sex or age composition can become fossilized in the same quarries for many different reasons (for example, death traps), realistic grouping patterns may be obscured. Data on sex, age, and reproductive status of wild (feral) horses (*Equus caballus*) that died in groups or individually on high altitude windswept ridges in the Great Basin Desert of North America indicate that (i) snow and mud are prominent forces influencing mortality and (ii) death in groups may be more common than has been assumed. This information has implications for determining some patterns of mortality in extant wild horse populations and assessing the validity of paleoethological reconstructions of social groupings.

Horses played prominent roles in community dynamics during the middle and late Tertiary in North America (*4*). Today, feral horses are conspicuous elements of the mammalian fauna of the Great Basin, where an estimated 35,000 to 40,000 range. Since 1979 I have studied populations of horses in the Granite Range of northwestern Nevada. Most horses migrate seasonally to the highest peaks, some of which exceed 2780 m. They are organized into distinct year-round bands, each with at least one stallion and a harem (females and young) (*5*). Nonharem males live alone or form bachelor groups.

The studied population has increased from 58 to 129, and 15 horses (yearlings or older) have disappeared. All individuals have been identified and the ages of more than 90 percent are known (*6*). Of the 15 animals that disappeared, the bodies or skulls of one bachelor male (9 years), three stallions (15+, 13, and 10 years), two younger males (2 and 3 years), five females (12, 6, 5, 5, and 4 years), and a male yearling have been located. Remains of nine of these animals (75 percent) were discovered along windswept ridgelines (Fig. 1A) at about 2600 m. From hair fragments of tails, manes, and fur, the animals were identified as members of two bands, last observed alive during the summer of 1979. One band of six animals (a male, 4 females, and a juvenile) was found in June 1981, and the other with three horses (two females and a juvenile), which had been part of a band of 12, was found in June 1982.

Three lines of evidence suggest not only that these two groups perished as a result of severe winter snowstorms but also that high altitude snow-induced mortality may be more common than has been assumed among some populations of mountain dwelling wild horses. First, because of their ages (*7*), one would not expect the dead animals to be in poor condition, and when last observed alive they appeared to be healthy and vigorous. Second, 80 to 85 percent of the animals migrated every year from winter ranges at low altitudes (around 1400 m) to higher altitudes for the summer and fall, where some remained into winter. The bands observed at high-altitude sites (2100 m, 2470 m, and 2560 m) during December 1980 and January 1981 were not subordinate bands and, thus, social factors did not appear to explain why they remained in summer ranges into early winter. Although it is likely that

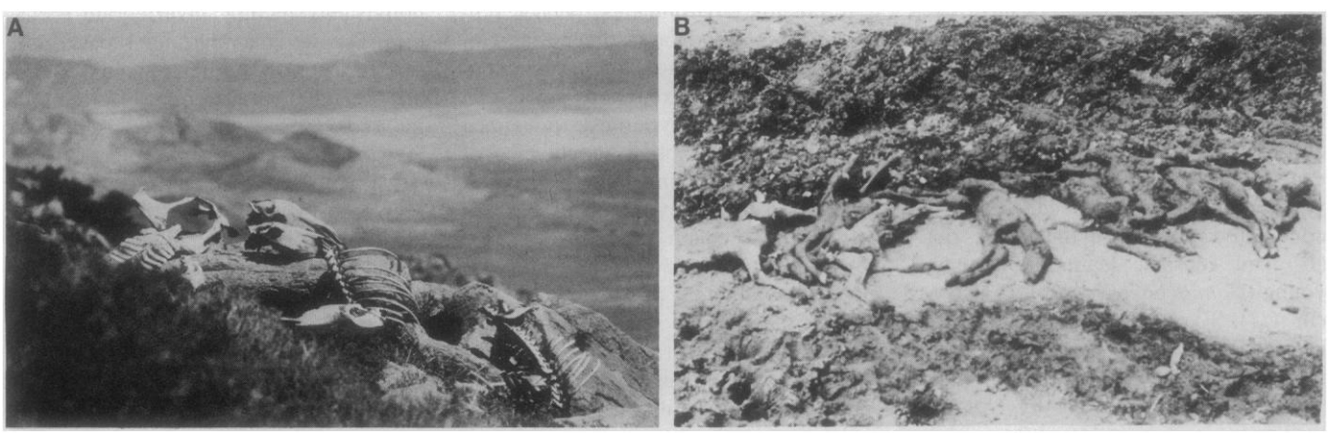

Fig. 1. (A) Skulls and skeletons on a ridge (about 2600 m) in the Granite Range, Nevada. Two of the skulls were removed from underlying vegetation and placed on rocks. (B) Foals in the Owyhee Desert, Nevada. Animals were pulled from the quagmire. [Desert photograph courtesy of the U.S. Department of the Interior]

these bands had access to high-quality food by remaining at the high altitudes they were also more likely to encounter severe winter snowstorms and cold. Third, the winter of 1979–80 (when these bands disappeared) was severe, and each of several snowstorms deposited over 65 cm of snow at about 1760 m. Accumulation at higher elevations and ridgelines, where the missing horses were found, would be much greater.

It is unlikely that snow was a density-dependent mortality factor, because of 42 skeletons located so far, 31 (74 percent) were situated above 2000 m and 28 (67 percent) were above 2300 m. The rest of the skeletons were found between 1400 and 2005 m. Because most horses spend less time at high altitudes (*6*), and all sites were searched for similar periods of time, the disproportionate number of bodies found at higher elevations [χ^2 (1) = 9.52; $P < .01$] suggests that unpredictably heavy snow accumulation is a principal mortality agent in the Granites as it may be elsewhere in the Great Basin. For instance, during the winter of 1977 an estimated 300 horses (50 percent of the population) died in the Buffalo Hills (*8*), an insular area 12 km west of the Granites. Although these animals existed at high densities (*8*), and individuals probably were in poor physical condition, it seems that snow precipitated the heavy mortality.

Drought is another factor that has contributed prominently in catastrophic mortality in Great Basin horses. For instance, the remains of nine young horses that died in mud apparently after following their mothers to drink were found in the Owyhee Desert of northern Nevada (Fig. 1B). The foals, from different bands and varying in age from 2 weeks to 2 months, and a yearling, were not able to pull themselves from the mud (*8*).

Similar death assemblages have been reported for other large extant mammals, although the extent to which catastrophic mortality influences demography is not known. Mud-induced die-offs occurred in zebras (*Equus zebra*) (*9*) and in cape buffalo (*Syncerus caffer*), the latter which "died at water's edge after becoming too weak to pull themselves out" (*10*) while massive deaths of wildebeest young (*Connochaetes taurinus*) also occur (*11*). Even mountain zebras have perished in sudden snowstorms in the mountains of South Africa (*12*).

Population size or density (*13*) may well be indirect mortality agents and are certainly important in determining spatial relations. However, weather related variables such as heavy snow accumulation apparently increase the susceptibility of entire groups to mortality and may be more debilitating to mountain dwelling Great Basin horses than once believed.

The data on mortality in Granite Range horses suggest that generalizations about the social structure of paleomammals from fossil assemblages should be made with caution. For instance, if nothing was known about the social organization of horses several different conclusions might have arisen had only one of the assemblages in the Granites been found. If the discovery was that of the two females and juvenile, it could be argued that females and young formed the only permanent associations for that species. However, if the stallion and his harem were located instead, the conclusion might be that bands were the primary social units. Thus although skewed sex and age ratios may indicate some aspect of sociality, there are limitations to the extent to which they can be used to reconstruct the social structure of fossil mammals.

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Reverse Diel Vertical Migration: An Escape from Invertebrate Predators

Abstract. *The marine copepod* Pseudocalanus *sp. exhibits an unusual reverse diel vertical migration in Dabob Bay, Washington, concurrently with a normal vertical migration by nocturnal invertebrate predators. Reduced spatial overlap with predators appears to decrease mortality rate of adult female* Pseudocalanus. *A life table analysis suggests that the demographic disadvantage associated with daily migration across a thermal gradient can be overcome if mortality is reduced by as little as 16 percent.*

In aquatic environments, pelagic representatives of phyla as diverse as cnidarians and chordates undertake conspicuous vertical excursions on a diel cycle. Among the hypotheses advanced to explain the adaptive significance of diel vertical migrations, three have broad application to the evolution of this behavior in the ocean and in lakes. Two concern metabolic (*1, 2*) or fecundity (*3*) advantages that may accrue to individual animals that migrate vertically when waters are thermally stratified. A third suggests that animals migrate to avoid visually feeding vertebrate predators (*4*).

We report that reverse diel vertical migration (nocturnal descent) allows a species of marine copepod to avoid nonvisually feeding invertebrate predators. This reverse migration recurs at the same location in different years and is not predictable by hypotheses other than the avoidance of nocturnal predators. A few instances of reverse migration behavior by zooplankton have been observed in marine (*5*) and freshwater (*6*) environments, although none in the ocean have been linked to predator-prey interactions.

At the deepest location (185 m) in Dabob Bay, a temperate fjord in Puget Sound, Washington (47°45'N, 122°49'W), which is oxygenated year-round, adult females of the small suspension-feeding copepod *Pseudocalanus* sp. (*7*) underwent a reverse diel vertical migration in