

# On the Pleistocene extinctions of Alaskan mammoths and horses

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The fossil record has been used to shed light on the late Pleistocene megafaunal extinctions in North America and elsewhere. It is therefore important to account for variability due to the incompleteness of the fossil record and error in dating fossil remains. Here, a joint confidence region for the extinction times of horses and mammoths in Alaska is constructed. The results suggest that a prior claim that the extinction of horses preceded the arrival of humans cannot be made with confidence.

radiocarbon dating | statistical inference | extinction times

The end of the Pleistocene was a period of large-scale megafaunal extinctions in North America and elsewhere (1). The factors responsible for these extinctions remain open to question, with climate change and hunting by humans among the leading candidates (2). According to Guthrie (3), “details of extinction timing are crucial in assessing competing theories about Pleistocene extinctions.” In using the fossil record for this purpose, it is common practice to identify the time of extinction of each taxon with the radiometric (or other) age of the most recent set of fossil remains. As discussed in more detail below, Guthrie (3) took this approach in analyzing the late Pleistocene fossil record of mammoths and caballoid horses in Alaska. He concluded that the extinction of the horse predated that of the mammoth by >1,000 years and, moreover, predated the arrival of humans, thereby ruling out the possibility that it was caused by hunting.

The age of the most recent remains is only a rough estimate of extinction time, and statistical methods are needed to determine how well extinction time is constrained by the fossil record. Such methods have been discussed in the paleobiological literature (4–6). Existing methods assume that the errors associated with dating fossil remains are negligible in relation to other sources of variability in the fossil record. Although this may be reasonable in some cases, it is not reasonable for late Pleistocene records, where dating error can be comparable in magnitude to the intervals between the ages of different sets of remains. The purpose of this paper is to describe a method for inference about the extinction times of two taxa that accounts for dating error in the fossil record and to apply this method to the data of Guthrie (3, 7). The results indicate that the possibility that the horse survived beyond the arrival of humans cannot be confidently ruled out.

## Results

Understanding the cause or causes of the late Pleistocene megafaunal extinctions in Alaska is particularly difficult. The difficulty arises from the confluence of two potentially important factors, a period of climate cooling known as the Younger Dryas and the arrival of humans from Asia. In an attempt to unravel the contributions of these factors, Guthrie (3) used radiocarbon ages of late Pleistocene fossil remains of mammoths (*Mammuthus primigenius*) and caballoid horses (*Equus ferus/caballus*) in Alaska to study the timing of the extinctions of these taxa. The most recent ages for mammoths and horses are 11.50 thousand radiocarbon years (ka) and 12.48 ka before present (ka

Table 1. Radiocarbon ages of the 25 most recent remains of caballoid horses and mammoths (3, 7)

Ages, ka BP	
Mammoth	Horse
11.50 (0.16)	12.48 (0.08)
11.54 (0.14)	12.51 (0.13)
11.91 (0.13)	12.56 (0.14)
12.12 (0.09)	12.58 (0.14)
12.19 (0.13)	12.71 (0.17)
12.34 (0.11)	12.86 (0.14)
12.43 (0.18)	13.25 (0.16)
12.44 (0.13)	13.27 (0.15)
12.48 (0.08)	13.94 (0.16)
12.49 (0.17)	14.00 (0.16)
12.51 (0.15)	14.12 (0.18)
12.58 (0.15)	14.26 (0.16)
12.68 (0.14)	14.30 (0.16)
12.88 (0.12)	14.62 (0.17)
13.06 (0.15)	14.99 (0.19)
13.23 (0.09)	15.37 (0.19)
13.29 (0.14)	15.50 (0.10)
13.34 (0.15)	15.57 (0.19)
13.38 (0.09)	15.75 (0.19)
13.41 (0.15)	15.92 (0.19)
13.44 (0.09)	16.13 (0.24)
13.66 (0.16)	16.15 (0.21)
13.69 (0.19)	16.48 (0.21)
14.02 (0.10)	16.70 (0.22)
14.09 (0.16)	17.65 (0.23)

Numbers in parentheses are SD in ka.

BP), respectively. Because these ages straddle the arrival time of humans in Alaska at around 12.00 ka BP, Guthrie (3) concluded that the “present Alaska data, showing that mammoths . . . survived more than a millennium after horses runs counter to extinction scenarios based on . . . human overhunting.”

Here, we apply the method described below to construct an approximate 0.95 joint confidence region for the extinction times  $\beta_1$  and  $\beta_2$  of mammoths and horses, respectively. The 25 most recent ages for each taxa, along with the standard deviations  $\sigma_j$  of the corresponding radiocarbon age errors, are reported in Table 1. These data were extracted from refs. 3 and 7. The oldest of these ages for horses is somewhat anomalous, lying almost 1.0 ka earlier than the next-oldest age, so it was omitted from the analysis. This omission had a negligible effect on the results. Thus, in this application, the numbers of samples are  $m = 25$  and

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Abbreviations: ka, thousand radiocarbon years; BP, ka before present; ML, maximum likelihood.

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$$X_j = U_j + \varepsilon_j \quad j = 1, 2, \dots, m, \quad [1]$$

where  $U_j$  is the true age, and  $\varepsilon_j$  is a normal radiocarbon dating error with mean 0 and known variance  $\sigma_j^2$ . Assume that the true ages  $U_1, U_2, \dots, U_m$  are independent and uniformly distributed over the interval  $(\beta_1, \gamma_1)$ , where the lower bound  $\beta_1$  corresponds to the time of extinction of the taxon. The uniform assumption is a strong one and should be checked. In general, it will not be valid over the entire fossil record and, in the next section, we will adopt it only for the most recent part of the record. It is straightforward to show that, under this model, the probability density function of  $X_j$  is:

$$f_j(x) = \frac{\Phi((x - \beta_1)/\sigma_j) - \Phi((x - \gamma_1)/\sigma_j)}{\gamma_1 - \beta_1}, \quad [2]$$

where  $\Phi$  is the standard normal distribution function. This model has been used for statistical inference about human settlement time based on the radiocarbon ages of archaeological remains (8). The presence of the normal dating error ensures that the regularity conditions underlying the basic likelihood theory hold. This is not the case in the absence of dating error.

Interest here goes beyond a single taxon to the relationship between the extinction times of two taxa. Accordingly, let  $Y_1, Y_2, \dots, Y_n$  be the radiocarbon ages of the remains of a second taxon, with

$$Y_j = V_j + \eta_j \quad j = 1, 2, \dots, n, \quad [3]$$

where  $V_j$  is the true age, and  $\eta_j$  is a normal dating error with mean 0 and known variance  $\tau_j^2$ . As with the first taxon, assume that the true ages are independent and uniformly distributed over the interval  $(\beta_2, \gamma_2)$ , where  $\beta_2$  is the extinction time of the second taxon. The probability density function of  $Y_j$  is:

$$g_j(y) = \frac{\Phi((y - \beta_2)/\tau_j) - \Phi((y - \gamma_2)/\tau_j)}{\gamma_2 - \beta_2}. \quad [4]$$

The two-taxon model can be used to address a variety of questions about the relationship between extinction times. Here, we focus on constructing a joint confidence region for  $\beta_1$  and  $\beta_2$ . As illustrated in the next section, this confidence interval is useful in understanding the relative timing of the two extinctions and their relationship to other events. The log-likelihood function for the two-taxon model is

$$L(\beta_1, \beta_2, \gamma_1, \gamma_2) = \sum_{j=1}^m \log f_j(x_j) + \sum_{j=1}^n \log g_j(y_j), \quad [5]$$

where  $x_j$  and  $y_j$  are the observed values of  $X_j$  and  $Y_j$ , respectively. The two terms on the right-hand side of (5) are the single-taxon log likelihoods for the first and second taxons, respectively. When, as here, interest centers on  $\beta_1$  and  $\beta_2$ , inference can be based on the profile log-likelihood function:

$$L(\beta_1, \beta_2) = L(\beta_1, \beta_2, \hat{\gamma}_1(\beta_1), \hat{\gamma}_2(\beta_2)), \quad [6]$$

where  $\hat{\gamma}_1(\beta_1)$  and  $\hat{\gamma}_2(\beta_2)$ , respectively, are the ML estimates of  $\gamma_1$  and  $\gamma_2$  found by maximizing Eq. 5 with  $\beta_1$  and  $\beta_2$  fixed.

Let  $\hat{\beta}_1$  and  $\hat{\beta}_2$  be the ML estimates of the two extinction times found by maximizing the profile log likelihood in Eq. 6. An approximate joint  $1 - \alpha$  confidence region for  $\beta_1$  and  $\beta_2$  is given by the set of values for which

$$2(L(\hat{\beta}_1, \hat{\beta}_2) - L(\beta_1, \beta_2)) \leq \chi_2^2(\alpha), \quad [7]$$

where  $\chi_2^2$  is the upper  $\alpha$  quantile of the  $\chi^2$  distribution with 2° of freedom.

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