A Multispecies Overkill Simulation of the End-Pleistocene Megafaunal Mass Extinction

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A computer simulation of North American end-Pleistocene human and large herbivore population dynamics correctly predicts the extinction or survival of 32 out of 41 prey species. Slow human population growth rates, random hunting, and low maximum hunting effort are assumed; additional parameters are based on published values. Predictions are close to observed values for overall extinction rates, human population densities, game consumption rates, and the temporal overlap of humans and extinct species. Results are robust to variation in unconstrained parameters. This fully mechanistic model accounts for megafaunal extinction without invoking climate change and secondary ecological effects.

More than half of the large mammal biota of the Americas disappeared in a cataclysmic extinction wave at the very end of the Pleistocene (1, 2). This dramatic event, unparalleled in the deeper fossil record and unmatched in other continents at the same time, has been attributed to the direct effects of human predation: the first solid evidence of large human populations in the Americas is at 13,400 years before the present (yr B.P.) (3), near the beginning of the extinction spasm, and humans are known to have hunted extinct megafauna (1, 2). Computer simulations of human population growth in the continental United States have been used to test the overkill model ever since Martin (1) first proposed it. Some of the key questions are whether population growth could have been sufficiently rapid (4), and hunting rates sufficiently high, to have driven 73% of large herbivore species into extinction (5–10).

Some human population growth models have not addressed the overkill problem directly (4, 11), whereas others have assumed a single, homogenized prey "species" (5–10) and have tested whether every last individual in this lumped population could have been exterminated. Ecological principles suggest that such a "total overkill" scenario is unlikely because of feedback between human and prey species population sizes (9); in any event, several large herbivore species did survive. The real questions, then, are whether a realistically scaled burst of human population growth could have resulted in a realistic number of extinctions, and whether such a model can correctly predict the extinction and sur-

vival of particular species on the basis of their ecological properties (1, 12). Here, I simulate human population growth, hunting patterns, and the population dynamics of 41 large mammalian herbivores—30 of them now extinct—across the Pleistocene-Holocene transition. The model tracks each species separately within each of 754 grid cells measuring 1° latitude by 1° longitude.

Many parameters and causal interactions could have been important in the extinction crisis, and the current model includes only the most clear-cut ones (13–28). Values that are known with reasonable certainty include differences among prey species in geographic ranges, body masses, and population densities; body mass–dependent differences among species in population growth rates; rates of production and caloric values of plant and small game (i.e., secondary) food resources; human nutritional needs; the maximal rate of increase of human populations; and the time of first appearance of substantial human populations in the United States.

Additional values that are not strongly constrained fall into four categories (28): (i) The initial number of humans entering the region was set at an absolute minimum of 100, following several previous studies (4, 7), and humans spread across the continent following a standard reaction-diffusion equation (4). (ii) Hunting ability was varied systematically (Table 1; trials 1 through 16 and 18 through 33) to determine the effect of different parameter values. The model mathematically implies that this parameter will strongly control the maximal rate of population increase and the ultimate population carrying capacity. Hunting effort was assumed to be nonselective and limited by food handling time and nutritional requirements (9, 21), so per capita kill rates never exceeded a

low ceiling. (iii) Competition among prey species for food might have had an indirect effect on extinction outcomes, so a master competition parameter was varied between extreme values (trials 34 through 43). (iv) Geographic dispersal of prey species was modeled in two opposed ways: with dispersal between grid cells forbidden for all species, and with complete annual mixing among cells, which implies high dispersal rates (trials 1 through 16 versus 18 through 33).

The simulation results are unambiguous (Fig. 1 and Table 1). Human population growth and hunting almost invariably leads to a major mass extinction. In fact, it is hard to find a combination of parameter values that permits all species to survive. These few scenarios (trials 1 through 3 and 18 through 21) require very low final human population densities of <0.13 people/100 km², an order of magnitude below the observed range for modern hunter-gatherers (4).

Furthermore, a single best-fit scenario (trial 8) simultaneously makes accurate predictions about extinction outcomes, extinction timing, and human ecology. It involves fast geographic dispersal of prey populations, full competition among prey species, and only modest rates of human hunting ability. It correctly predicts the fates of 32 out of 41 species (78%). The exceptions are six "surviving" species that actually are extinct and three "extinct" species that actually survive (Fig. 1).

By comparison, predicting survival strictly on the basis of body mass by declaring all species heavier than 180 kg to be extinct would identify 23 of 30 extinct and 7 of 11 surviving species, for a prediction success rate of 73%. This too is significantly better than a random guess ($G = 4.020$, $P < 0.01$). Thus, the mechanistic model does succeed in replicating the observed pattern of differential extinction across the body mass spectrum (1, 2, 12), but without making any ad hoc assumptions about human preferences for large game. Indeed, additional simulations demonstrate that the only way to prevent a size-selective mass extinction is to assume that humans strongly prefer to hunt small game.

Extinction times are another accurate prediction of the best-fit model (Fig. 1). The median extinction occurs 1229 years after the initial invasion of humans. The earliest is at 801 years, and all but three take place by 1640 years. These figures amount to dozens of human generations, far longer than the normal span of oral history. Furthermore, it takes 260 years for the human population to exceed 1000 individuals, and 410 to exceed 10,000, so we might not expect the archaeological record to show evidence of humans before those times. Thus, a 1000- to 1200-year overlap of humans and megafauna might

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Table 1. Results of simulation trials. Simulations are run over 2500 years, and human populations are seeded at 49°N, 114°W, except where noted. Preferred simulation trial (trial 8) is in bold. "Trial" = trial identification number; "Hunting ability" = coefficient in units of 10^{-6}; "c" = coefficient regulating competition among herbivore species; "Growth rate" = maximum per-year rate of growth of human population; "Max density" = maximum population density in people/100 km²; "End density" = final population density in people/100 km²; "Meat in diet" = proportion of calories obtained by hunting large mammalian herbivores; "Energy use" = relative amount of primary production in calories consumed by herbivores, given as a proportion of the starting value; "Actually exinct" and "Actually surviving" = simulated extinctions of actually extinct and surviving species, with counts of species predicted to be extinct and (followed in parentheses) inviable at the end of each trial (inviable = final population <100 and declining); "True fates" = minimum total of correct extinction and survival predictions (maximum = 30 + 11); "Median extinction" = median time to extinction in years for species going extinct before the end of the simulation. Significance value is based on a G-test of a 2-by-2 contingency table, with inviable species treated as surviving; similar results are obtained if these species are treated as extinct. * = $P < 0.05$; ** = $P < 0.025$; *** = $P < 0.01$; **** = $P < 0.005$.

Trial	Hunting ability	c	Growth rate	Max density	End density	Meat in diet	Energy use	Actually extinct	Actually surviving	True fates	Median extinction
					Fast dispersal of prey species						
1	24	1.0	1.15%	5.22	0.03	0.360	0.985	0 (0)	0 (0)	11	N/A
2	26	1.0	1.25%	6.17	0.05	0.319	0.980	0 (0)	0 (0)	11	N/A
3	28	1.0	1.35%	7.07	0.13	0.281	0.973	0 (1)	0 (0)	11	N/A
4	30	1.0	1.42%	7.92	0.32	0.239	0.959	2 (2)	0 (0)	13	1338
5	32	1.0	1.49%	8.71	0.69	0.182	0.932	5 (6)	0 (0)	16	1094
6	34	1.0	1.55%	9.47	1.79	0.150	0.871	13 (6)	0 (2)**	22	1498
7	36	1.0	1.61%	10.18	3.74	0.132	0.762	21 (2)	2 (1)***	29	1411
8	**38**	**1.0**	**1.66%**	**10.86**	**5.82**	**0.111**	**0.638**	**24 (0)**	**3 (0)***	**32**	**1229**
9	40	1.0	1.70%	11.52	7.70	0.088	0.515	24 (1)	3 (1)***	31	1092
10	42	1.0	1.74%	12.14	9.45	0.067	0.398	25 (0)	4 (0)**	32	1007
11	44	1.0	1.78%	12.75	11.04	0.047	0.288	26 (1)	4 (2)***	31	948
12	46	1.0	1.81%	13.34	12.51	0.027	0.184	27 (1)	6 (1)*	31	892
13	48	1.0	1.84%	13.95	13.87	0.008	0.086	28 (0)	7 (2)	30	842
14	50	1.0	1.87%	16.21	16.21	0.004	0.045	29 (0)	11 (0)	29	820.5
15	52	1.0	1.90%	18.55	18.55	0.001	0.016	29 (0)	11 (0)	29	776.5
16	54	1.0	1.92%	20.80	20.80	0.000	0.000	30 (0)	11 (0)	30	751
					Duration of trial 14,000 years						
17	38	1.0	1.66%	10.86	5.84	0.111	0.637	25 (0)	4 (0)**	32	1284
					No dispersal of prey species						
18	24	1.0	1.14%	4.12	0.00	0.222	1.000	0 (0)	0 (0)	11	N/A
19	26	1.0	1.25%	4.93	0.00	0.178	1.000	0 (0)	0 (0)	11	N/A
20	28	1.0	1.33%	5.70	0.01	0.151	1.000	0 (1)	0 (0)	11	N/A
21	30	1.0	1.41%	6.46	0.03	0.136	0.999	0 (5)	0 (0)	11	N/A
22	32	1.0	1.48%	7.21	0.18	0.127	0.992	3 (9)	0 (0)	14	2331
23	34	1.0	1.54%	7.98	0.79	0.120	0.963	7 (6)	0 (1)	17	1470
24	36	1.0	1.59%	8.78	2.30	0.109	0.891	12 (8)	1 (2)	20	1427
25	38	1.0	1.64%	9.65	4.55	0.096	0.778	19 (2)	3 (3)	24	1459
26	40	1.0	1.68%	10.63	6.97	0.081	0.647	21 (0)	4 (2)	26	1341
27	42	1.0	1.72%	11.72	9.22	0.065	0.514	23 (1)	6 (0)	28	1234
28	44	1.0	1.75%	12.90	11.25	0.049	0.385	24 (1)	6 (0)	29	1108.5
29	46	1.0	1.79%	14.18	13.02	0.033	0.263	24 (1)	6 (0)	29	1007
30	48	1.0	1.82%	15.54	14.74	0.018	0.156	27 (0)	7 (0)	31	966.5
31	50	1.0	1.85%	17.00	16.60	0.008	0.075	27 (1)	8 (0)	30	926
32	52	1.0	1.87%	18.64	18.61	0.002	0.022	28 (0)	9 (0)	30	898
33	54	1.0	1.90%	20.81	20.81	0.000	0.002	29 (0)	9 (1)	30	862
					Varying competition among prey species						
34	38	0.0	1.66%	12.88	6.65	0.121	0.314	11 (1)	0 (0)*	22	975
35	38	0.1	1.66%	12.08	6.36	0.119	0.391	13 (2)	0 (0)**	24	927
36	38	0.2	1.66%	11.74	5.85	0.114	0.453	14 (1)	0 (0)***	25	1034
37	38	0.3	1.66%	11.53	5.39	0.108	0.508	15 (1)	0 (2)***	26	1113
38	38	0.4	1.66%	11.37	5.34	0.105	0.543	17 (4)	0 (2)****	26	1200
39	38	0.5	1.66%	11.24	5.49	0.107	0.564	20 (1)	2 (0)**	29	1291.5
40	38	0.6	1.66%	11.14	5.63	0.108	0.581	21 (2)	2 (0)***	30	1259
41	38	0.7	1.66%	11.05	5.74	0.109	0.596	22 (1)	2 (1)****	30	1243.5
42	38	0.8	1.66%	10.98	5.81	0.110	0.609	22 (1)	2 (1)****	30	1217.5
43	38	0.9	1.66%	10.92	5.84	0.111	0.622	24 (0)	2 (1)****	32	1228
					Initial invasion point 32°N, 112°W (Arizona)						
44	38	1.0	1.87%	10.75	5.82	0.111	0.638	24 (1)	3 (0)***	32	1043
					Initial invasion point 25°N, 80°W (Florida)						
45	38	1.0	1.90%	9.05	5.82	0.111	0.638	24 (1)	3 (1)***	31	1334
					Initial invasion point 42°N, 73°W (Connecticut)						
46	38	1.0	1.57%	10.10	5.82	0.111	0.638	25 (0)	4 (0)**	32	1339
					Initial population seeded uniformly						
47	38	1.0	1.61%	11.99	4.68	0.114	0.728	20 (3)	3 (1)	27	1324

be expected. The earliest appearance of Clovis artifacts in the United States is at about 13,400 yr B.P. (3); the very youngest calibrated ^{14}C dates on extinct megafauna are around 12,260 yr B.P. (25). The known overlap is therefore some 1200 years, roughly as predicted. On the basis of the early Clovis date and the model's population dynamics, humans are predicted to have arrived south of the Laurentide ice sheet in low numbers between 13,600 and 13,800 yr B.P.

Several scenarios similar to the best-fit one (Table 1; trials 7 through 9) also yield realistic extinction percentages (56 to 71%, depending on how inviable species are categorized), highly statistically significant predictions about extinction outcomes ($P <$ 0.01), and entirely reasonable predictions about human ecology. These scenarios not only assume modest maximal population growth rates of about 1.61 to 1.70%/year, but imply equilibrial population densities of 3.7 to 7.7 people/100 km^2, with about 8.8 to 13.2% of human dietary needs (i.e., 194 to 290 kcal/person/day or about 64 to 97 g meat/person/day) being met by hunting large game. Temperate-zone deserts, prairies, and forests have median population densities of 3 to 8 people/100 km^2 (4); modern hunter-gatherers consume 43 to 290 g of meat/person/day (29). Meanwhile, scenarios with excessive hunting success rates (trials 14 through 16) imply extreme densities of up to 21 people/100 km^2 and lead to the extinction of all, or almost all, large game species. Scenarios assuming poor hunting ability (trials 1 through 6) generate unrealistic population densities of <2 people/100 km^2 and high (if still plausible) large game consumption rates of up to 264 g meat/person/day.

Of the parameters that were varied across simulations, hunting ability is the most important. Increasing this parameter by a factor of two (trial 1 versus trial 13) causes final

human population densities to increase by a factor of >500. This is true even though the peak rate of population increase varies only between 1.14 and 1.92%/year across all the simulation trials. Extinctions always ensue if hunting ability is sufficient to generate human population densities of >0.2 people/100 km^2. Relatively high hunting ability can lead to the extinction of all but one or two large herbivore species, even when final human population densities are barely over the observed range (e.g., trial 14).

Direct competition for food among prey species plays a minor role (Table 1; trials 34 through 43). Complete independence of prey populations leads to somewhat lower overall extinction rates, but human population dynamics and the discrimination of truly extinct and surviving species are largely insensitive to this parameter. Higher values may be more realistic, because large-sized terrestrial herbivores are known to compete for food resources even with rodents (30). Therefore, the other simulations assume full competition.

Geographic dispersal of prey species is not a key factor with respect to any of the human population parameters or to the overall extinction rate (trials 1 through 16 versus trials 18 through 33). However, it does undergird the model's ability to predict the fate of individual species. For trials with intermediate hunting coefficients, no-dispersal simulations do still imply higher rates of extinction for actually extinct species than one would expect at random, and lower rates for actually surviving species (trials 24 through 26). However, these differences are not significant (Table 1). Meanwhile, in the comparable fast-dispersal runs, discrimination is always highly significant (trials 7 through 9). The difference involves a few geographically restricted species like *Palaeolama mirifica* that go extinct only with fast dispersal, perhaps because of large population swings me-

diated by indirect competition. In any event, the contrast here is between a very unrealistic no-dispersal case and an idealized, but still imaginable, case of fast annual dispersal that prevents visible gradients in population densities.

Most of the simulations depict a human invasion proceeding from the northwest corner of the continent [i.e., a "blitzkrieg" (6–8)]. To test for any effect of this assumption, grid cells in Arizona, Florida, and Connecticut also were designated as the initial point of invasion (trials 44 through 46). These three simulations all yield comparable extinction patterns. By contrast, a completely uniform seeding of the initial human population across the continent (trial 47) still leads to a major mass extinction, but predicts individual extinctions more poorly. Thus, the mass extinction per se was inevitable given the general facts of human ecology, but individual species outcomes may have hinged on indirect competition being mediated by a gradual human invasion.

The simulations predict that total human population size might have overshot its carrying capacity during the extinction event. The magnitude of the resulting boom-and-bust cycle varies substantially. If hunting ability is very poor, the population crashes by >99% (trial 1); in the best-fit scenario, the crash is only 46% (trial 8, Fig. 1); with very high final population densities, there is no crash (trials 14 through 16). In any event, a relatively mild bust phase might not register clearly in the archaeological record, and a substantial overshoot is not needed to predict a realistic extinction (trial 11).

A skewed distribution of extinction times is consistently seen across the simulations (Fig. 1). Extinctions fall into three cohorts: a first wave within 1000 years; a second wave over the next few hundred years, including most of the true megafauna; and a third wave
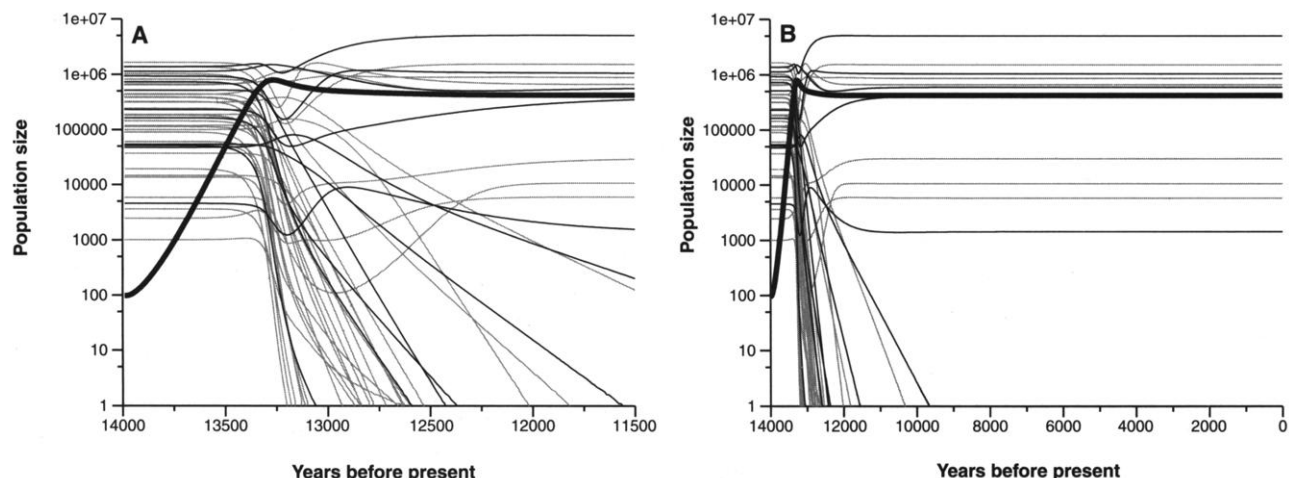
Fig. 1. Population dynamics of human and prey species. Preferred trial is shown (Table 1; trial 8). Thick black lines = human population; thin black lines = 11 actually surviving species; thin gray lines = 30 actually extinct species. (**A**) First 2500 years of the human invasion during the terminal Pleistocene. (**B**) Entire 14,000 years following human invasion, spanning the terminal Pleistocene and Holocene.

including a few stragglers. Extinction dates are primarily governed by rates of increase, geographic range size, and population density. A few medium-sized Gulf Coastal Plain endemics like *Palaeolama mirifica* and *Tapirus veroensis* seem to fall in the second cohort only when the usual human invasion point is in the far northwest. However, these species always do go extinct, and most other slowly disappearing species were more widely distributed. The strikingly skewed temporal pattern disagrees with the assumption that proboscideans should have gone extinct well before other taxa (*31, 32*); to the contrary, here, proboscideans are all victims of the second extinction wave. Unfortunately, testing for such small differences in timing is not likely to be fruitful, given current limitations on carbon dating (*3*).

A final point of interest is the impact of human hunting on the overall rate of consumption of plant resources by herbivores (Table 1). The more realistic scenarios all imply that at equilibrium, human predation would depress rates of herbivory in energetic terms by about one-quarter to one-half (trials 7 through 9). If accurate, these figures imply a major disruption of ecosystem function at the continental scale, with potentially severe consequences for vegetational structure, the size of vegetational carbon sinks, watershed dynamics, insect and small vertebrate population dynamics, and so on.

Many complicating factors are ignored by the model. Several involve aspects of human biology and history: selective human hunting of individual prey species (*31*); human-induced habitat change; the possible introduction of pandemic diseases to native herbivore species by humans (*33*); and the possibility that instead of expanding quickly from a small founding population, humans actually were present at low densities long before the extinction. By and large, adding these factors to a model should increase extinction rates, decrease the required human population growth and carrying capacity values, and possibly increase the model's ability to predict the extinction of actually extinct species. For example, four small-sized, common, and mostly wide-ranging species (*Capromeryx minor*, *Mylohyus fossilis*, *Platygonus compressus*, and *Stockoceros conklingi*) are predicted to have survived in trial 8, but are actually extinct today. These extinctions may relate to human hunting preferences, genetically based lack of flight responses (*34*), or perhaps vulnerability to disease organisms. Ignoring such factors simply makes the model more conservative.

A suite of other complicating factors involves nonhuman ecological patterns and processes: demographic stochasticity; genetic "meltdown" at small population sizes; short-

term environmental stochasticity (*32*); variation among geographic regions in the availability of secondary food resources (*4*); ecological feedbacks introduced by populations of nonhuman predator species; habitat change induced by extinction of keystone herbivore species (*31*); and direct biological effects of long-term climate change (*35, 36*). Several of these factors would only increase extinction rates, especially for rare species. For example, northern temperate zone ungulates are known to respond strongly to decadal-scale climate variability (*20*), so short-term climate events might have delivered the coup de grace to steeply declining species.

Some of the more problematic features of the model could be explained by these additional factors. For example, the survival of three large-sized species is not easily predicted: *Alces alces*, *Bison bison*, and *Cervus elaphus*. All three extended their ranges far into Canada during the early Holocene as the Laurentide ice sheet collapsed (*13*). The survival of *B. bison* also may relate to lower human population densities in the dry steppe and prairie of the northern Great Plains (*4*), where edible secondary food resources may have been less abundant. Finally, pairs of geographically overlapping, morphologically similar, and phylogenetically related extant and extinct species might have experienced stronger pairwise competition than was modeled (e.g., *A. alces* versus *Cervalces scotti*; *B. bison* versus *B. priscus*).

The improved, ecologically realistic model outlined here challenges the common-sense notion that no amount of overkill could have resulted in a true megafaunal mass extinction. The simulations demonstrate not merely that overkill scenarios are plausible, but that an anthropogenic extinction was unavoidable given the facts of ecology and the fossil record—even assuming that human predation was limited and nonselective. The overkill model thus serves as a parable of resource exploitation, providing a clear mechanism for a geologically instantaneous ecological catastrophe that was too gradual to be perceived by the people who unleashed it.

References and Notes

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28. Geographic ranges were based on minimum convex polygons around occurrences of fossils in the FAUNMAP database (*13*). Body mass values were based on published estimates (*14–16*) and published skeletal measurements combined with standard allometric equations (*17*). Initial population densities of species were inferred as a joint function of the standard mammalian body mass/density scaling relationship (*18*) and observed frequencies of occurrence, using a back-calculation that assumes sampling is a Poisson process. Prey population dynamics were modeled following the standard Ricker logistic growth equation, with standard coefficients for mammals (*19*); logistic density dependence is known to be strong in northern temperate zone ungulates (*20*). Standard logistic equations were used to model secondary food resources (*9, 13, 21*). Human nutritional needs were set to 2200 kcal/person/day, and the ratio of materials gathered to materials consumed was set conservatively to 1.4 (big game) and 4.2 (secondary resources). Human hunting and gathering ability was modulated by a type 2 functional response (*26*), capping both maximum intake and maximum success at 1.4 standard rates. Human population growth was modeled as an exponential function of the ratio of actual to standard caloric intake, assuming a theoretical maximum of 3%/year (*4, 7, 9, 11, 24, 25*). Simulations ran from 14,000 yr B.P. to 11,500 yr B.P., encompassing the earliest Clovis dates [13,400 yr B.P. (*3*)] and terminal faunal dates [>12,260 yr B.P. (*26*)]. Interspecific competition was treated using a standard Lotka-Volterra model that employs the Ricker logistic equation, with population sizes weighted according to Kleiber's law of metabolic scaling (*27*). Details are available at www.sciencemag.org/cgi/content/full/292/5523/1893/DC1.
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