that support the scenario of drought of subtle variability with high impact. In addition, the data and modeling support an interpretation of decreased rainfall during the summer, associated with a reduction in the severity and frequency of tropical storms. This study suggests that there is substantial potential for establishing a relationship between the actual climatic variability over the region and the spatially complex historical events (30) that shaped the demise of the Maya civilization.

References and Notes
18. Materials and methods are available as supporting material on Science Online.

Evolution of the Earliest Horses Driven by Climate Change in the Paleocene-Eocene Thermal Maximum
Ross Secord,1,2 Jonathan L. Bloch,2 Stephen G. B. Chester,3 Doug M. Boyer,4 Aaron R. Wood,5,2 Scott L. Wing,6 Mary J. Kraus,7 Francesca A. McInerney,8 John Krigbaum9

Body size plays a critical role in mammalian ecology and physiology. Previous research has shown that many mammals became smaller during the Paleocene-Eocene Thermal Maximum (PETM), but the timing and magnitude of that change relative to climate change have been unclear. A high-resolution record of continental climate and equid body size change shows a directional size decrease of ~30% over the first ~130,000 years of the PETM, followed by a ~76% increase in the recovery phase of the PETM. These size changes are negatively correlated with temperature inferred from oxygen isotopes in mammal teeth and were probably driven by shifts in temperature and possibly high atmospheric CO2 concentrations. These findings could be important for understanding mammalian evolutionary responses to future global warming.

Interest in how organisms respond to climate change has intensified in recent years with projected warming of ~2°C to 4°C over the next century (1). Although models can be developed to predict evolutionary responses to warming of this magnitude, empirical examples must be drawn from fossil or historical records. Here we report a dramatic example of shifts in body size in the earliest known horses (family Equidae) during the Paleocene-Eocene Thermal Maximum (~56 million years ago). The PETM is recognized in marine and continental records by an abrupt negative carbon isotope excursion (CIE) that lasted ~175 thousand years (ky), caused by the release of thousands of gigatons of carbon to the ocean-atmosphere system (2, 3). Some marine records suggest that although δ13C values shifted rapidly at the onset of the CIE in 21 ky or less (2), temperature increase was slower, peaking 60 ky or more into the CIE (4) at ~5°C to 10°C above pre-CIE levels (5, 6). We use oxygen isotope values in mammal teeth as a proxy for local temperature change in the continental interior of North America, and we show that equid body size during the PETM was negatively correlated with temperature.

In extant mammals and birds (endotherms), closely related species or populations within a species are generally smaller-bodied at lower latitudes, where ambient temperature is greater (7). This relationship, known as Bergmann’s rule, is followed by ~65 to 75% of studied extant mammals (8, 9). The cause of Bergmann’s rule is usually attributed to thermoregulation and the optimization of body size (10) and/or the availability of food resources related to primary productivity (11). Bergmann’s rule predicts that average mammalian body size should decrease with warming climate, and smaller size in endotherms has even been suggested as a third “universal” response to warming, along with changes in phenology and species distribution (12). Declining body size has been attributed to warming over decadal and millennial scales in some living endotherms (12, 13), but many counterexamples also exist (10). Furthermore, it is difficult to distinguish natural selection (genetic change) from ecophenotypic plasticity (morphological response

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not genetically fixed) over such short time scales. The size change documented here was, however, sustained over thousands of generations, strongly suggesting that natural selection was the cause.

Previous studies lacked the stratigraphic resolution to recognize patterns in body size change within the PETM but demonstrated gross changes in size in several mammalian lineages, based on first molar tooth area (14, 15). Size changes occurred in herbivorous ungulates (Perisodactyla, Artiodactyla, Condylarthra, and Tillodontia), Primates, and faunivores and omnivores (Cromodonta, Carnivora, and Palaeoherbivora), affecting both immigrant and endemic taxa (Fig. 1). These changes conform well to Bergmann’s rule in terms of the expected direction of size change. Quantifying published results, size reduction occurred in 10 Paleocene genera that ranged into the PETM, representing 38% of the range-through genera. This was followed by post-PETM size increases in eight of these genera, indicating that body size response was strongly taxon-specific (Fig. 1 and table S7). Post-PETM size increases also occurred in an additional eight genera, seven of which first appeared in the PETM (Fig. 1). Together these 16 genera represent a size increase in 40% of PETM genera that ranged into post-PETM biozone Wa-1 (Fig. 2).

*Sifrhippus* (formerly *Hyracotherium* (16)) first appeared in North America and Europe during the PETM. Because of the lack of a plausible ancestor on these continents, it is widely thought to be an immigrant that crossed high-latitude dispersal routes opened by PETM warming (17). We use *Sifrhippus* to document mammalian body size change within the PETM. *Sifrhippus* is the most abundantly represented genus in new collections from the Cabin Fork area (~10 km²) of the southern Bighorn Basin, Wyoming, and the only one for which detailed stratigraphic and quantitative morphological data are available. We also isotopically sampled *Sifrhippus*, *Coryphodon* (Pantodontia; large archaic herbivorous ungulates), and *Ectocion* and *Copecon* (phacodontid condylarths; herbivorous ungulates of uncertain affinities). The PETM at Cabin Fork is represented by a ~35-m-thick sequence of fluvial mudstones, floodplain soils (paleosols), and fluvial sandstones. We constructed an age model that presents by a ~35-m-thick sequence of fluvial mudstones, floodplain soils (paleosols), and fluvial sandstones. We constructed an age model that

![Fig. 1. Summary of percent mean body size change in genera that exhibit change from the latest Paleocene to the PETM (left), and from the PETM to the post-PETM (right). No genus exhibits a size increase in the PETM or a decrease after the PETM. Compiled from published sources, except for *Sifrhippus* from this study. Asterisks indicate genera that first appear in the PETM. See table S7 for a summary of all PETM taxa and sources.](https://www.sciencemag.org/content/335/6061/960/F1.large.jpg)

To test whether body size change in *Sifrhippus* is significantly correlated with temperature, as predicted by Bergmann’s rule, we used δ18O values in *Coryphodon* enamel (δ18Oe as a proxy for change in mean annual temperature (MAT). *Coryphodon* was a large water-dependent or semiaquatic mammal (21, 23). Studies of ecologically similar living mammals have shown that their δ18Oe faithfully records the δ18O of surface water (24, 25), which in turn is strongly correlated with air temperature at mid- to high latitudes (26). *Sifrhippus* has been used as a proxy for change in mean annual temperature (MAT). *Coryphodon* was a large, water-dependent or semiaquatic mammal (21, 23). Studies of ecologically similar living mammals have shown that their δ18Oe faithfully records the δ18O of surface water (24, 25), which in turn is strongly correlated with air temperature at mid- to high latitudes (26).

Greater aridity in the PETM could also have contributed to diminished body size by lowering primary productivity. Both floras and paleosols in the Bighorn Basin suggest increased aridity during at least parts of the PETM (6, 20, 27). To test this, we used two aridity proxies. The first is based on the difference between mean δ18Oe values in aridity-sensitive and aridity-insensitive mammals (24). *Coryphodon* should be aridity-insensitive because of its probable water dependence (21, 23), whereas *Sifrhippus* is the taxon most likely to be aridity-sensitive, because it has the highest average mammalian δ18Oe value, suggesting that it consumed leaves in open areas where leaf water was evaporatively 18O-enriched. Increased aridity should result in higher δ18Oe values and greater separation between it and *Coryphodon* δ18Oe (Fig. 3A). Our second aridity proxy estimates mean annual precipitation (MAP) based on paleosol major oxides (Fig. 3C and SOM).
correlative section (HW16 section, SOM).

95% confidence of the aridity. Error bars show difference implies greater temperatures in the Neotropics (weakened above ~11°C and reverses at higher temperature). Overall, there is poor agreement between Sifrhippus into the PETM). Overall, there is poor agreement between Sifrhippus and Coryphodon. (B) Aridity proxy curve based on (A), showing mean differences between Sifrhippus and Coryphodon. Greater difference implies greater aridity. Error bars show 95% confidence of the mean, offset in (A) by 1 m to avoid overlap. (C) MAP proxy based on paleosol major oxides from a nearby correlative section (HW16 section, SOM).

Both proxies suggest drier conditions at the beginning of the CIE, followed by wetter conditions starting at ~20 m (~68 ky into the PETM), with a return to drier conditions by ~38 m (~108 ky into the PETM). Overall, there is poor agreement between Sifrhippus body size change and the aridity proxies. Both proxies indicate a shift to wetter conditions while body size in Sifrhippus is decreasing, which is counter to expectations if the primary cause of dwarfing was lowered productivity caused by increased aridity.

Our results are consistent with mammalian dwarfing driven by warming, but temperature alone may be an insufficient explanation. Although body mass in living mammals is highly correlated with MAT in the Nearctic [coefficient of determination ($R^2 = -0.75$)], this relationship weakens above ~11°C and reverses at higher temperatures in the Neotropics (9). MAT was well above ~11°C in the latest Paleocene and PETM of the Bighorn Basin (6). Furthermore, ~25 to 35% of living mammals deviate from Bergmann’s rule (8, 9), and it is likely that at least some mammal lineages would have gotten larger during the PETM if MAT were the only controlling factor.

Another possible cause for body size decrease in the PETM is elevated atmospheric partial pressure of CO$_2$ (PCO$_2$) (28), which might covary with temperature. In many extant plants, elevated CO$_2$ could have been a contributing factor, our results favor temperature as the primary driver of dwarfing in Sifrhippus. PETM warming was similar in magnitude to that predicted by some global models over the next century (11) but occurred at a much slower rate and began from a warmer late Paleocene baseline. Nevertheless, some generalizations applicable to future warming may still be relevant. Diminished body size in some mammal species, along with changes in ecology and physiology, might be expected in response to warming. The pattern of dwarfing seen in the PETM mirrors recent reductions in body size in endotherms that have been attributed to anthropogenic warming (10, 12). Although the rate of present warming is much faster than during the PETM, and mammals may not respond in exactly the same manner, the dramatic response to warming observed in PETM equitoes provides a measure of possible responses to future warming in modern mammals.

References and Notes
One-Time Transfers of Cash or Capital Have Long-Lasting Effects on Microenterprises in Sri Lanka

Suresh de Mel,1 David McKenzie,2,4 Christopher Woodruff3

Standard economic theory suggests that one-time business grants can have at most temporary effects, and accordingly, policies to increase incomes of the self-employed in developing countries typically rely on sustained engagement. In contrast, we found long-lasting impacts from one-time grants given in a randomized experiment to subsistence firms. Five years after we gave $100 or $200 to 115 of 197 male and 190 for female-owned firms, we found 10-to-$12-per-month-higher profits for male-owned businesses that received the grants. Female-owned businesses showed no long-term (or short-term) impacts. Our follow-up investigation interviewed 94% of the original sample and collected survivorship data from the remaining 6%, demonstrating that tracking long-term outcomes is both feasible and worthwhile. The results suggest that one-off grants may have lasting impacts on some types of subsistence firms, challenging the view that sustained engagement is always required.

One-time grant to small business owners have any long-term effect? Traditional economic models of firm investment such as the Ramsey model predict that there is an efficient size for a business, conditional on the owner’s ability level. Any shock to capital in this model will have only temporary effects, and the firm will quickly return to the steady state. In such a model, an extra infusion of capital in the business can speed up convergence to this steady-state efficient size but cannot have any long-term effect ($\delta$).

In contrast, a one-off infusion of capital can have a permanent impact on business investment if there are poverty traps or under-investment caused by production nonconvexities (in which the only profitable investments are lumpy ones, such as buying a large machine, and where it may be not be possible to operate a business if capital falls below some threshold level) ($\delta$); if there are self-control problems and time-inconsistent preferences (for example, in which today an individual prefers to spend the money that tomorrow he or she reinvests profits in the business, but when tomorrow comes prefers to spend the money) ($\delta$, $\Omega$); or if there are intra-household inefficiencies (for example, owners may underinvest when they expect proceeds to be taken by a spouse or other family members) ($\delta$, $\Omega$). Knowing whether the traditional models or these alternatives best describe

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Table 1. Impact of the grants on business survival rates and reporting profits. Data are ordinary least squares results of the impact of the grant on (i) whether the business was closed in 2010, as measured in the June 2010 and December 2010 survey rounds and by observation and proxy reports for firms not interviewed, and (ii) whether it reports profits in either survey round. Robustness to excluding proxy reporting is shown in table S2. Sample size is 197 for male-owned firms and 190 for female-owned firms. Huber-White SE are shown in parentheses.

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