

**Evolution of the Earliest Horses Driven by Climate Change in the Paleocene-Eocene Thermal Maximum**Ross Secord, *et al.**Science* **335**, 959 (2012);

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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.

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Supporting Online Material

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Evolution of the Earliest Horses Driven by Climate Change in the Paleocene-Eocene Thermal Maximum

Ross Secord,^{1,2*} Jonathan I. 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° 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 (PETM) (~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° 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 (10). 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

¹Department of Earth and Atmospheric Sciences, University of Nebraska, Lincoln, NE 68588, USA. ²Florida Museum of Natural History, University of Florida, Gainesville, FL 32611–7800, USA. ³Department of Anthropology, Yale University, New Haven, CT, 06520, USA. ⁴Department of Anthropology and Archaeology, Brooklyn College, City University of New York, New York, NY 11210, USA. ⁵Department of Geology and Geological Engineering, South Dakota School of Mines and Technology, Rapid City, SD 57701, USA. ⁶Department of Paleobiology, Smithsonian Museum of Natural History, Washington, DC 20560, USA. ⁷Department of Geological Sciences, University of Colorado, Boulder, CO 80309, USA. ⁸Department of Earth and Planetary Sciences, Northwestern University, Evanston, IL 60208, USA. ⁹Department of Anthropology, University of Florida, Gainesville, FL 32611–7305, USA.

*To whom correspondence should be addressed. E-mail: rsecord2@unl.edu

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 mammal lineages, based on first molar tooth area (14, 15). Size changes occurred in herbivorous ungulates (Perissodactyla, Artiodactyla, Condylarthra, and Tillodontia), Primates, and faunivores and omnivores (Creodonta, Carnivoramorpha, and Palaeonodonta), 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 *Copecion* (phenacodontid 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 assumes varying rates of sediment accumulation: Avulsion deposits (mudstones and thin sandstones) represent fast rates, and paleosols represent much slower rates [see the supporting online material (SOM)]. Local sections were correlated to a composite section (Fig. 2) using marker beds traced with a differential Global Positioning System unit (SOM).

The CIE at Cabin Fork is recorded in the carbonate component of mammalian tooth enamel ($\delta^{13}\text{C}_\text{E}$) (Fig. 2, A and B) and in bulk organics and leaf wax *n*-alkanes (6, 18). $\delta^{13}\text{C}_\text{E}$ in mammalian herbivores reflects the $\delta^{13}\text{C}$ value of the vegetation they consume, with predictable enrichment (19). Plants in turn track the $\delta^{13}\text{C}$ value of atmospheric CO_2 , with influences from environ-

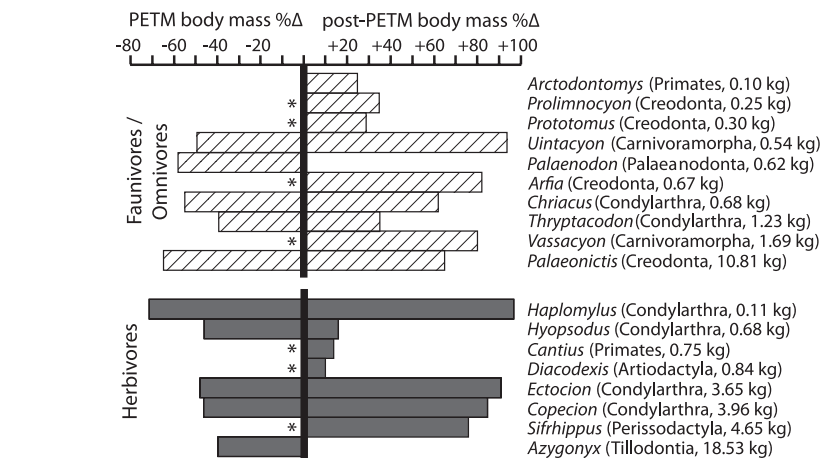


Fig. 1. Summary of percent mean body size change in genera that exhibit change from the latest Paleocene to the PETM (left), and from the PETM to the post-PETM (right). No genus exhibits a size increase in the PETM or a decrease after the PETM. Compiled from published sources, except for *Sifrhippus* from this study. Asterisks indicate genera that first appear in the PETM. See table S7 for a summary of all PETM taxa and sources.

mental factors such as humidity and vegetation density (20, 21). At Cabin Fork, phenacodontids (*Ectocion* and *Copecion*) record a negative shift of ~4.6 per mil (‰) in $\delta^{13}\text{C}_\text{E}$ at the onset of the CIE (Fig. 2A). This is consistent with estimates of atmospheric change of ~4.6‰ during the PETM from a leaf discrimination model (20) and ~4.0‰ from modeling of marine carbonate dissolution (2), indicating that phenacodontid $\delta^{13}\text{C}_\text{E}$ is primarily tracking atmospheric $\delta^{13}\text{C}$ values, rather than environmental change.

Sifrhippus sandrae first appears at Cabin Fork near the base of the lowest intermittent red bed (LIRB) at 14.5 m (Fig. 2). The onset of the CIE in most mammal teeth also begins at the base of the LIRB (Fig. 2, A and B) but is recorded slightly lower (13.75 m) in dispersed bulk organics. The oldest specimens of *S. sandrae* had an average body size of ~5.6 kg, based on first lower molar area (SOM). Body size in *S. sandrae* progressively decreased from its first appearance at 14.5 m to the 41-m level, with a total reduction of ~30% over ~130 ky ($P < 0.001$) (Fig. 2D and SOM). Individuals at 41 m had an average body weight of ~3.9 kg and are among the smallest known horses. The dwarfing of *S. sandrae* was followed by a ~76% increase in body size during the recovery phase of the CIE, to an average size of ~7.0 kg (Fig. 2D).

The mode of evolution (random, static, or directional) for *Sifrhippus* body size change was determined using a moving window log rate interval (mwLRI) analysis, which is a modification of the standard LRI analysis (22) (SOM). Both methods assume that rates of change in a time series variable are inversely proportional to the interval of time over which rates are measured, because of the occurrence of small reversals in the variable. The relationship between rates of change and the lengths of intervals over which they are observed is used to determine evolutionary mode (22). Our mwLRI results indicate

with 95% confidence that *Sifrhippus* body size directionally decreased from its first appearance to the 41-m level, after which stratigraphic resolution and sample sizes are insufficient to distinguish between directional and random evolutionary change. Thus, *Sifrhippus* experienced sustained selection for diminutive body size for ~130 ky.

To test whether body size change in *Sifrhippus* is significantly correlated with temperature, as predicted by Bergmann's rule, we used $\delta^{18}\text{O}$ values in *Coryphodon* enamel ($\delta^{18}\text{O}_\text{E}$) as a proxy for change in mean annual temperature (MAT). *Coryphodon* was a large water-dependent or semi-aquatic mammal (21, 23). Studies of ecologically similar living mammals have shown that their $\delta^{18}\text{O}_\text{E}$ faithfully records the $\delta^{18}\text{O}$ of surface water (24, 25), which in turn is strongly correlated with air temperature at mid- to high latitudes (26). *Sifrhippus* first lower molar area is negatively correlated with *Coryphodon* $\delta^{18}\text{O}_\text{E}$ values ($P \leq 0.05$, SOM), suggesting that *Sifrhippus* body size decreased as ambient air temperature increased.

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 $\delta^{18}\text{O}_\text{E}$ 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 $\delta^{18}\text{O}_\text{E}$ value, suggesting that it consumed leaves in open areas where leaf water was evaporatively ^{18}O -enriched. Increased aridity should result in higher *Sifrhippus* $\delta^{18}\text{O}_\text{E}$ values and greater separation between it and *Coryphodon* $\delta^{18}\text{O}_\text{E}$ (Fig. 3A). Our second aridity proxy estimates mean annual precipitation (MAP) based on paleosol major oxides (Fig. 3C and SOM).

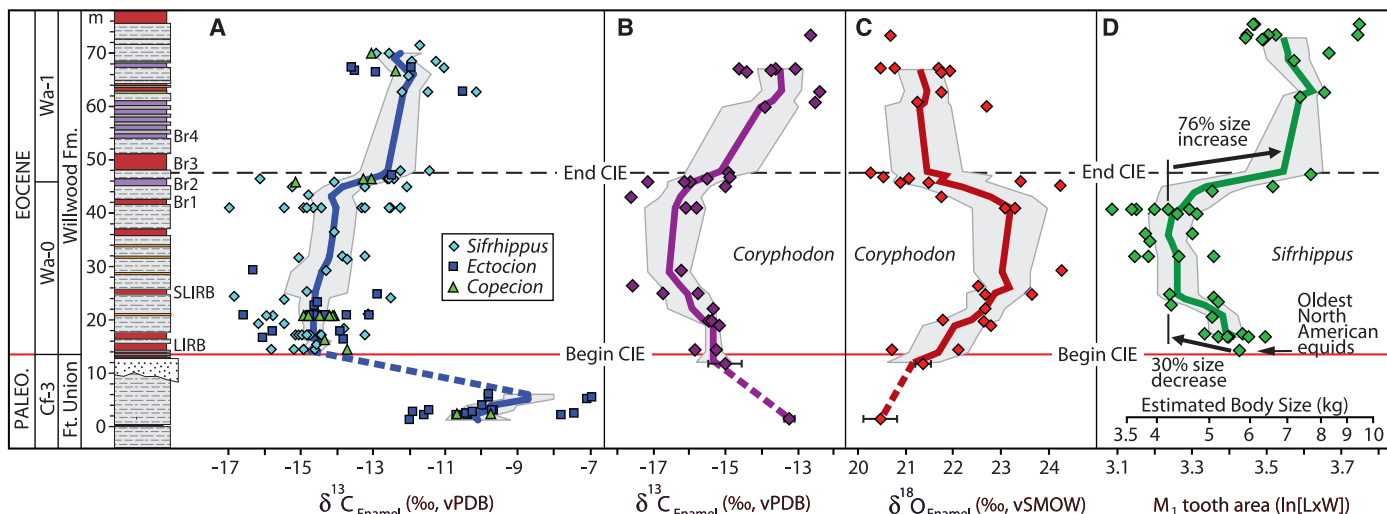
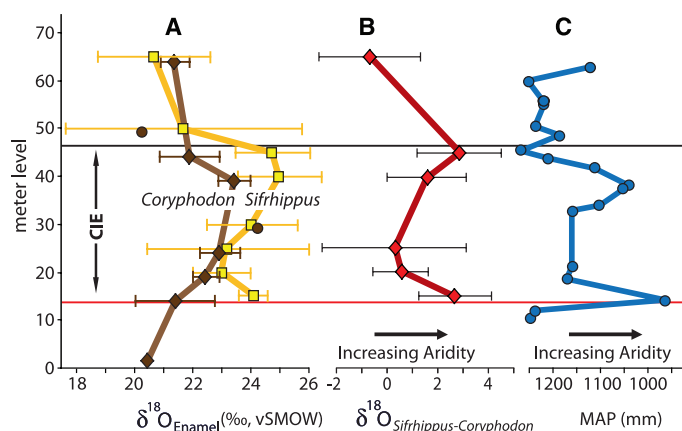


Fig. 2. Comparison of PETM Cabin Fork records. (A) From left to right, epochs, mammalian biozones, formations, meter levels, marker beds, and $\delta^{13}\text{C}_\text{Enamel}$ values for three common mammal genera. vPDB, Vienna Pee Dee belemnite standard. (B and C) $\delta^{13}\text{C}_\text{Enamel}$ and $\delta^{18}\text{O}_\text{Enamel}$ values for *Coryphodon*. vSMOW, Vienna standard mean ocean water standard. (D) Log-transformed measurements of first lower molar area (length \times width) for *Sifrhippus*.

Data points represent single individuals except where error bars (indicating 95% confidence of the mean for multiple samples from one individual) are shown. Solid colored lines show five-point moving averages; the gray area is the 95% envelope of uncertainty for each line. PALEO, Paleocene; Cf, Clarkforkian; Wa, Wasatchian. LIRB, SLIRB, and Br denote key marker beds.

Fig. 3. Aridity and precipitation proxies.



(A) Comparison of mean $\delta^{18}\text{O}_\text{E}$ values for aridity-insensitive *Coryphodon* (brown diamonds) and aridity-sensitive *Sifrhippus* (gold squares). Data are in 5-m bins. Brown circles are singletons of *Coryphodon*. (B) Aridity proxy curve based on (A), showing mean differences between *Sifrhippus* and *Coryphodon* $\delta^{18}\text{O}_\text{E}$. 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 $\sim 11^\circ\text{C}$ and reverses at higher temperatures in the Neotropics (9). MAT was well above $\sim 11^\circ\text{C}$ 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 (P_{CO_2}) (28), which might covary with temperature. In many extant plants, elevated CO_2 increases biomass but reduces nitrogen and protein content in leaves and can elevate phenol levels, yielding cellulose-rich vegetation that is less nutritious and harder for herbivores to digest (29). Ultimately, this should result in slower growth and reproductive rates in herbivorous mammals (30), conceivably resulting in selection for smaller body size. Although this mechanism could have reduced body size in herbivores, size also decreased among PETM carnivores (Fig. 1), which must be explained by an indirect response, such

as selection for smaller predators because of smaller prey (31). Recent modeling of rates of carbon release during the PETM shows the largest increase in P_{CO_2} at the onset of the CIE, followed by lower concentrations later in the event (2). This is inconsistent with a P_{CO_2} -driven decrease in body size, because *Sifrhippus* was smallest near the end of the main phase of the PETM. Although elevated P_{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 (1) 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, mammals may not respond in exactly the same manner, the dramatic response to warming observed in PETM equids provides a measure of possible responses to future warming in modern mammals.

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Supporting Online Material
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One-Time Transfers of Cash or Capital Have Long-Lasting Effects on Microenterprises in Sri Lanka

Suresh de Mel,¹ David McKenzie,^{2*} 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 100 of 190 female Sri Lankan microenterprise owners, we found 10-percentage-point-higher enterprise survival rates, and \$8-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.

Self-employment is one of the major sources of income for the urban poor across the world, with between 47 and 69% of poor (per capita income less than \$2 per day) households in urban areas in Indonesia, Pakistan, Peru, and Nicaragua running a business (1), most often without paid employees. Typical policies to improve the incomes of these households and their businesses are based on sustained provision of services. Three such programs are (i) microfinance, which is often based on the expectation of a succession of loans, and in many cases regular follow-up meetings with clients in groups (2–4); (ii) conditional cash transfer programs, which typically give households regular transfers over a period of years (5, 6); and (iii) business training programs, which

are based on the idea that capital alone is not enough—as in the ancient proverb “give a man a fish and he eats for a day, teach a man to fish and he can feed himself for life”—with some evidence suggesting that training works best when accompanied by one-on-one follow-up visits (7).

But can just giving a fish feed a man for life? That is, does the much simpler policy of giving a

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 (8).

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) (9); if there are self-control problems and time-inconsistent preferences (for example, in which today an individual prefers that tomorrow he or she reinvests profits in the business, but when tomorrow comes prefers to spend the money) (8, 10); 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) (8, 11). Knowing whether the traditional models or these alternatives best describe

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. *, **, and *** denote impact is significantly different from zero at the 10, 5, and 1% levels, respectively.

	Males		Females	
	Closed	Reports profits	Closed	Reports profits
Treatment amount (in 10,000s of LKR)	−0.109*** (0.0401)	0.0876** (0.0378)	0.0252 (0.0558)	−0.0176 (0.0546)
Control group mean	0.29	0.77	0.26	0.77

¹Department of Economics, University of Peradeniya, Peradeniya 20400, Sri Lanka. ²Development Research Group, The World Bank, Washington, DC 20433, USA. ³Department of Economics, University of Warwick, Coventry CV4 7AL, UK.

*To whom correspondence should be addressed. E-mail: dmckenzie@worldbank.org.