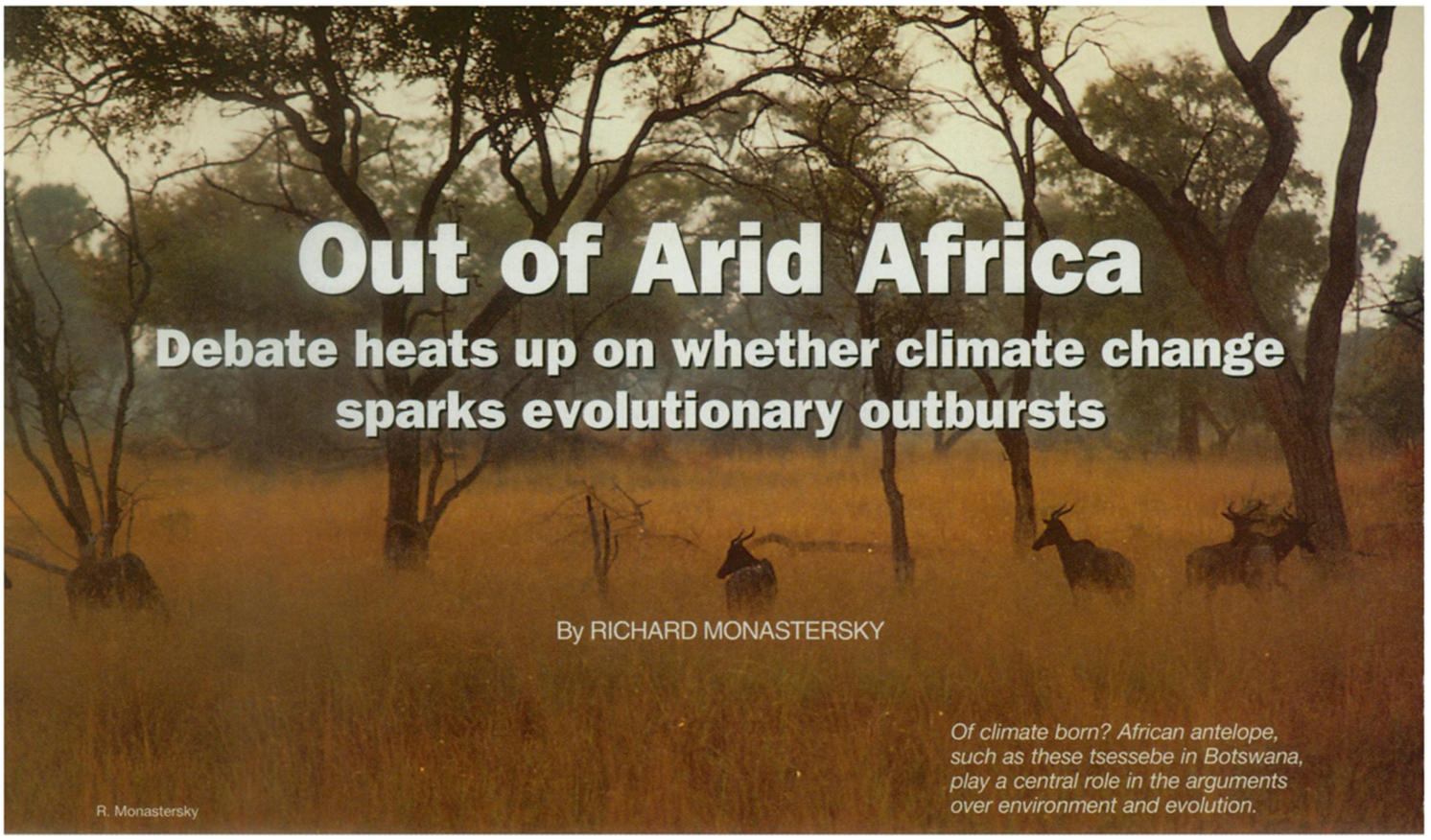

Out of Arid Africa

Debate heats up on whether climate change sparks evolutionary outbursts

By RICHARD MONASTERSKY

Of climate born? African antelope, such as these tsessebe in Botswana, play a central role in the arguments over environment and evolution.

R. Monastersky

Something strange started happening to the world around 2.5 million years ago. In the far north, the once balmy climate turned bitter as glacial sheets advanced over the landscape and icebergs started bobbing in the Atlantic. In the Andes of South America, forests disappeared and grasslands took over as the weather turned cooler and drier. In northwest Africa, an infant desert started gobbling up acreage en route to becoming the vast Sahara. In southern and eastern Africa, increasing aridity withered woodlands and helped savannas spread.

Amid all this ecological change, a group of erect apes underwent a burst of evolution that led eventually to the appearance of the genus *Homo*.

Coincidence or not? That is the question raised by a provocative idea called the turnover pulse hypothesis, proposed in 1985 by paleontologist Elisabeth Vrba of Yale University. The theory holds that species tend to remain stable until the environment changes, triggering rapid spells of extinctions and originations.

The hypothesis reaches far beyond the origin of human ancestors and addresses the broad sweep of biological upheavals throughout time. Darwin saw competition between individuals as the primary engine driving evolution. While not denying the role of competition, Vrba looks to an external agent, broadly defined as climate change, as the instigator of major evolutionary spasms.

Shifting rainfall, fluctuating sea levels, erupting volcanoes, and the wanderings of the continents all combine, through their effects on the environment, to set the pace at which species appear and disappear. Vrba says that climate sparks these evolutionary changes by breaking up habitats, causing populations of animals to become separated from other members of their own species.

Although intriguing and controversial, the turnover pulse hypothesis went largely untested for many years. Now, paleontologists are challenging the hypothesis using rigorous statistical examinations of the fossil record. If theories live and die like species, then the current scrutiny may determine whether Vrba's hypothesis thrives, goes extinct, or evolves into a new form.

Vrba lays out the case for the idea in two chapters in *Paleoclimate and Evolution, with Emphasis on Human Origins* (Yale University Press), which came out this spring. Because the fossil record of humans and their direct kin includes fewer than a dozen species, it is a poor choice to use in testing the turnover pulse hypothesis. So Vrba has turned to the African bovids, a family of ruminants whose best-known living members include the antelopes.

Bovids, she argues, make a good testing ground for the turnover pulse hypothesis because they are usually the most plentiful large mammal at African fossil sites—a fact readily understood by anyone who has watched film footage of the great wildebeest migration across the Serengeti. Vrba has compiled a database of 147 African bovid species reaching back over the last 14 million years.

Africa, as some biologists have noted, is antelope heaven, with 72 different species currently bounding around the continent. To trace the ascendancy of the antelopes and other bovids, Vrba tallied the first appearance of each species at 41 sites in 10 nations.

During the Pliocene epoch, from 5.3 million to 1.6 million years ago, one period stood out as a time of exceptional expansion in this family. Within the interval 2.7 million to 2.5 million years ago, the number of species surged by 44, far more than for any other period. Among the newcomers during this interval were several that survive today, including the greater kudu, roan antelope, blue duiker, and the oryx.

Even accounting for gaps in the fossil record, which can make appearances seem to cluster in time, Vrba finds that the pulse remains strong. Of the 44 species that debuted as fossils during this key interval, she estimates that only 12 may actually have evolved during previous gaps.

The acceleration in evolution at this time also bred a different type of antelope, notes Vrba. Before 3 million years ago, the majority of new bovids appearing in Africa were adapted to warmer, moister, and more wooded environ-

ments. But between 2.7 and 2.5 million years ago, the number of new species adapted to colder or arid conditions increased relative to previous times.

"The late Pliocene bovid evidence taken together is consistent with a turnover pulse that started 2.8 million years ago and is seen in the record by 2.7–2.5 million years and that was initiated by a major cooling trend," she states in *Paleoclimate and Evolution.*

From the firm ground of the bovid data, Vrba leaps into the spindly branches of the human family tree and asks whether hominids—*Homo sapiens* and our nearest extinct relatives—experienced a similar pulse.

Although the fossil record of hominids is sketchy and anthropologists agree on few details, the available evidence does support the idea of a pulse in speciation at this time, asserts Vrba. Sometime around 2.8 million years ago, *Australopithecus afarensis*, which includes the fossil widely known as Lucy, split into at least two lineages, *Australopithecus africanus* and *Australopithecus aethiopicus.*

A third group may have appeared then as well. Anthropologists have found remnants of stone tools—considered the handiwork of *Homo*—in deposits 2.5 million years old (SN: 4/15/95, p. 237). Although they have yet to find clearly identifiable *Homo* fossils in rocks of that age, researchers suspect that our genus may have first appeared more than 2.5 million years ago.

Speciation among hominids at this time also bears the stamp of a changing environment. *A. aethiopicus* had enlarged molars and premolars and beefed-up chewing muscles, mouth specializations that are often viewed as adaptations for eating tough grasses rather than the softer fruits of the woodlands. The newer hominids also sported larger bodies than their predecessors, and biologists find that body size tends to increase as the climate grows colder.

These and other observations, says Vrba, support her contention that climatic change between 2.8 million and 2.5 million years ago triggered pulses of evolution among hominids, bovids, and other African mammals.

Other paleontologists, however, discern a strikingly different picture of evolution when they look at that period.

Anna K. Behrensmeyer and her colleagues at the Smithsonian Institution in Washington, D.C., have tested Vrba's idea by examining fossil records for the Lake Turkana basin in Kenya and Ethiopia. This region has the advantage of containing the best-dated rock formations for the critical time period in Vrba's work.

As part of the Smithsonian's Evolution of Terrestrial Ecosystems Program, Behrensmeyer and her coworkers used statistical tests to analyze the extinctions and originations of mammals at 342 sites in the Turkana basin. Whether they assigned questionable fossils to separate species or lumped them into known species, they found no statistically significant pulse of extinctions or originations between 2.8 and 2.5 million years ago. Neither bovids nor mammals as a whole underwent massive changes during this 300,000-year span, they report.

These mammals did experience significant turnover, but it dragged out over the entire interval between 3 million and 2 million years ago, Behrensmeyer reported in June at the Sixth North American Paleontological Convention in Washington, D.C.

"We wouldn't contest that there's something important going on ecologically and evolutionarily and that it is probably related to global climate change. The sticking point is that it's a revolutionary pulse at 2.8 to 2.5," she says.

"The image that has gotten out there is that there was suddenly this demise of the forests and the woodlands, the opening of the savannas, and the hominids striding out into this brand-new, open country—with all this happening in a fairly short geological period of 300,000 years. There just doesn't seem to have been this kind of urgency to the transition."

John Harris, a bovid specialist at the Natural History Museum of Los Angeles County, could not find a short turnover pulse during Vrba's critical period either. Harris, the former head of paleontology at the National Museums of Kenya, examined records of bovids and other ungulates in the Turkana Basin for the period 2 million to 4 million years ago as part of a broad study, published in 1991. "We came to the conclusion that there was no support in the Turkana Basin for a major turnover in the fauna at about 2.5 million years ago," he says.

Both Behrensmeyer and Harris restricted their studies to the rocks of the Turkana Basin, whereas Vrba looked at fossils from all over Africa. This may explain the divergent results, because species from southern Africa might have been more susceptible to the climatic cooling, admits Behrensmeyer.

Differences in approach also appear important, however, particularly in the choosing of fossil ages. Some of the fossils in Vrba's analysis, especially those in South Africa, are not well dated, making it difficult to relate the ages of these fossils to those found elsewhere, says Harris.

The turnover pulse hypothesis fares no better in studies reaching further back in time. John Alroy, a paleontologist at the University of Arizona, tested the idea in his analysis of 3,900 mammal fossil sites in North America over the last 55 million years. Alroy broke the time span into 1-million-year intervals and computed how species extinctions and originations varied throughout this period.

"What I found was there was no support for the major predictions of the hypothesis on this timescale," he says.

Vrba's theory predicts that climate change should affect disparate groups of animals by triggering a round of extinctions and then speciations within a limited time. Alroy's analysis suggests no relationship in North America between surges in extinction rates and bursts in evolution. What's more, he finds that different animals experienced evolutionary pulses at very different times.

Alroy calls the turnover pulse idea "very, very reasonable. It's a very intuitive hypothesis." But his analyses, "taken together, make it pretty hard to argue for turnover pulses in the North American mammal record at the timescale of a million years."

Donald R. Prothero of Occidental College in Los Angeles took a different tack but nevertheless reached similar conclusions. He looked through the North American mammal record to see how species responded to three periods of extreme climate change during the last 40 million years: a global cooling during the Eocene epoch, 37 million years ago; a severe cooling in the early Oligocene, at 33 million years ago; and a drying in the Miocene at 7.5 million to 7 million years ago.

Although many marine and some land creatures apparently suffered during these climatic crises, North America's mammals weathered them with little change, Prothero reported at the Washington meeting. "In the three big cases, there was no real turnover pulse," he says.

Prothero's study, like most of the other tests, has yet to go through the peer-review process and appear in published form. If these studies hold up to further scrutiny, however, they will undermine Vrba's hypothesis, at least in its present incarnation, says Behrensmeyer.

Even if the turnover pulse hypothesis falters, it need not bring down the idea that climatic upheavals have shaped human evolution. This broader concept, popular among paleontologists, has spawned several recent books, including *Humanity's Descent* (William Morrow, 1996) by Smithsonian paleontologist Richard Potts and *Children of the Ice Age* (Harmony Books, 1996) by Steven M. Stanley of Johns Hopkins University.

Yet faced with the lack of firm evidence, many paleontologists prefer to duck the debate and retreat to the rocks, where they know the answer lies. "My first thought," says Behrensmeyer, "is let's keep looking for fossils." □