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News and Views

Did the super-eruption of Toba cause a human population bottleneck? Reply to Gathorne-Hardy and Harcourt-Smith

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Introduction

Gathorne-Hardy and Harcourt-Smith raise questions about the accuracy of estimates of the magnitude of the climatic impact of the supereruption of Toba, whether it could have caused a human population bottleneck, the form, duration and timing of the human bottleneck, and cultural capacities for behavioral responses to climatic disasters. This News and Views forum provides an opportunity to summarize the new geological, climatic and genetic evidence for the super-eruption of Toba and its consequences that supports our hypothesis (Ambrose 1998a; Ambrose and Rampino, 2000), and to address other critiques and alternative explanations (Oppenheimer, 2002; Lahr and Foley, 1998; Hawks et al., 2000).

The super-eruption of Toba and its global climatic impacts

Toba is now the world's largest volcanic crater lake. The pyroclastic flows of the outer slopes cover $>20,000 \text{ km}^2$, and reach the southwest and northeast shores of northern Sumatra. The crater

* Tel.: 217-244-3504 E-mail address: ambrose@uiuc.edu (S.H. Ambrose). was formed in an explosive eruption dated to 73.5 ka (thousand years ago) by K/Ar (Chesner et al., 1991), and 71 ka by ice core chronology (Zielinski et al., 1996).

How big was the Toba eruption? Martin A.J. Williams first recognized the Toba ash in terrestrial sedimentary sequences in north-central India (Williams and Royce, 1982; Shane et al., 1995; Westgate et al., 2000). By 1991, it had been found in deep sea cores west and north of Sumatra, as far as the Bay of Bengal. The dense rock equivalent (DRE) volume of volcanic ash blasted into the atmosphere by Toba was estimated to be 800 km³ (Huff et al., 1992). To put this volume in perspective, the largest known explosive eruption of the last 450 million years, which occurred during the Ordovician, had an estimated DRE of 1100 km³. Tambora, the largest historically recorded eruption, had a DRE of 20 km³, and was apparently responsible for the year without a summer in 1816 (Stothers, 1984). Krakatau, on which Gathorne-Hardy and Harcourt-Smith rely to assess the impact of Toba, had a DRE of only 15 km3 (Huff et al., 1992).

Reports of the distribution of Toba ash published since 1993 now show its *minimum* extent encompassed the northeastern Arabian Sea (64° east) (Schulz et al., 2002), the Indian Ocean, 14° south of the equator (Pattan et al., 1999), northern

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India and Bangladesh, 25° north of the equator (Acharyya and Basu, 1993; Gasparatto, et al., 2000; Westgate et al., 1998), and ~113° east, in the South China Sea (Buhring et al., 2000; Song et al., 2000; Huang et al., 2001). The minimum area of the ash from this eruption, and thus its DRE volume, are thus now substantially larger than previously estimated.

Gathorne-Hardy and Harcourt-Smith question the magnitude of the eruption and its environmental impacts because Mentawi island, located 350 km southwest of Toba, has a primate and termite fauna that was apparently not destroyed by hot debris from this eruption. However, no direct effects should be expected, because this island, as well as the rest of Sumatra and Java, were directly upwind of, and thus insulated from, the eruption (see Oppenheimer 2002: Fig. 2).

Huang et al., (2001) chronicle the climatic impact of the eruption on the South China Sea, and summarize evidence for its correlation with other global climate records. An abrupt 1°C drop in the temperature of the South China Sea occurred immediately above the Toba ash (Huang et al., 2001). The highest frequencies of ice-rafted debris in the 95,000 year long record of the North Pacific Ocean were recorded at \sim 72 ka (Kotilaninen and Shackleton, 1995). In the Greenland GISP2 ice core, the largest amount of volcanic sulfur in the 110,000-year record occurs at 71 ka, and is attributed to Toba (Zeilinski et al., (1996). This massive sulfur peak spans six or seven years, confirming the original estimates of a sulfur aerosol-induce sixyear volcanic winter proposed by Rampino and Self (1992, 1993). This sulfur peak is immediately followed by the largest peak of calcium in the GISP2 core, which represents a 200-year period of unusually high amounts of windblown dust, probably due to decreased vegetation density and exposure of sediments as sea levels dropped. Zeilinski et al. (1996) estimate that the temperature dropped >6°C over Greenland, based on oxygen isotope ratios. Lang et al. (1999), based on nitrogen isotope ratios of trapped air bubbles, conclude that temperature abruptly increased approximately 16°C (28°F) from this low point in the ice record to a temperature similar to that of other warm

periods of the last ice age. In each of these records, the largest temperature drop of the late Pleistocene coincides with the Toba eruption, and in each it lasted for 1000 to 2000 years.

Several parameters of the Toba eruption have been critically evaluated by Oppenheimer (2002), who notes that there is a large range of uncertainty in estimates of eruption volume, height of eruptive plume, duration of the eruption, and amount and duration of stratospheric sulfur aerosol. Because the greatest climatic impact of an eruption is due to the reflectance of solar radiation by stratospheric sulfur, rather than by ash particles, which settle from the atmosphere rapidly, uncertainty about the SO₂ parameter generates the greatest uncertainty in the effect on global temperatures. However, given the growing body of evidence for a severe short-lived climatic event in several kinds of records (Huang et al., 2001), and the obviously awesome size of this eruption, especially the sulfur record in the GSP2 ice core (Zeilinski et al., 1996), the low end of the ranges of estimates of any eruptive parameters seem improbable.

Both Oppenheimer (2002) and Gathorne-Hardy and Harcourt-Smith use ice core oxygen isotopic evidence to assert that the magnitude and duration of the temperature drop at 71 ka was similar to that of the remaining 18-19 millennial-scale oscillations during the last ice age. However, they appear to have relied on the graphic presentations of smoothed data in published figures (for example, Zeilinski et al., 1996: Fig. 1), in which the ice core δ^{18} O values were averaged over approximately 400 years. Time averaging of the data makes it appear that there was only a relatively brief period of extreme cold in the middle of this stadial event. However, inspection of the high resolution oxygen isotope record, for example in Fig. 1 of Lang et al. (1999), which has a ~ 40 year resolution, shows that the cold event at 70-71 ka was consistently coldest for its entire duration, and had the longest duration of all such events in the 110 ka ice core record. The ice core geochemical record shows that the pattern of enhanced cooling for several centuries after the eruption of Toba does not occur in other stadial events (Zeilinski, 2000).

Bottlenecks: large or small, early or late, long or short, putative or real?

Uncertainties in the size and duration of the "putative" bottleneck are emphasized bv Gathorne-Hardy and Harcourt-Smith. Virtually all studies of the genetic structure of living human populations that have analyzed the history of past population size implied by this structure, have identified a significant late Pleistocene human population bottleneck. Many studies were cited previously (Ambrose, 1998a). With one significant exception cited by Gathorne-Hardy and Harcourt-Smith (i.e., Hawks and Wolpoff, 2000), this recent bottleneck, or more precisely, expansion from a very small population size in Africa, continues to be consistently identified (Forster et al., 2001; Gagneux et al., 1999; Harpending and Rogers, 2000; Jin et al., 1999; Jorde et al., 1998; Marth et al., 2002; Pritchard et al., 1999; Qamar et al., 1999; Quintana-Murci et al., 1999; Rogers, 2001; Takahata et al., 2001; Underhill et al., 2000; Thompson et al., 2000; Watkins et al., 2001). Two major bottlenecks/expansions occurred soon after the African bottleneck. (Jin et al., 1999; Oamar et al., 1999; Quintana-Murci et al., 1999; Underhill et al., 2000; Zeitkiewicz et al., 1998). These are likely to be founder effects of small populations leaving Africa (Ambrose 2003; Lahr and Foley 1998). It is clear that the African bottleneck occurred prior to, but close in time to these colonization bottlenecks. African populations increased from a very small size, approximately 70,000 years ago (Jorde et al., 1998). It is this population bottleneck that is attributed to the climatic impact of Toba (Ambrose, 1998a, 2003; Ambrose and Rampino, 2000).

If the African bottleneck did not occur at this time, but was a result of climatic factors, when could it have occurred? It is highly unlikely to have occurred during the favorable climatic regime of the last interglacial, oxygen isotope stage 5, between ~130 and 71 ka. It would either have endured for the entire last glacial, which ended only 12 ka, or during the previous glacial period, marine oxygen isotope stage 6, 190–130 ka. Lahr and Foley (1998) argue that this climatic bottleneck was actually caused by the harsh environmental conditions of the penultimate glacial period (oxygen isotope stage 6), in part based on the assumption of a date of ~240 ka for African Eve (Cann et al., 1987). However, if more recent and accurate estimates of the human coalescent date for modern humans of ~135 ka are correct (Stoneking et al., 1992), then the age of expansion from the bottleneck, which is halfway between Eve and the present (Harpending et al., 1993), is consistent with the volcanic winter hypothesis (Ambrose, 1998a). Population densities were undoubtedly low during stage 6, which is consistent with the coalescent age of African Eve.

Gathorne-Harding and Harcourt-Smith cite Hawks et al. (2000) to reject the hypothesis of a bottleneck. However, Hawks et al. (2000) clearly conflate the origin of species with a population bottleneck. In other words, they assert that bottlenecks must also be speciation events. Based on their assumption that *Homo erectus* and its descendants should all be classified as *Homo sapiens* (Hawks et al., 2000, p. 3), they date the bottleneck to approximately 2 million years ago. Their estimate of the bottleneck age, the assumptions on which it is based, and their hominid taxonomy, are so remarkably discordant with other studies that they cannot be considered realistic.

Was the bottleneck long or short? Determining the duration of a bottleneck is extremely difficult because a comparatively short, extremely severe bottleneck cannot be differentiated from a longer, less restricted one (Relethford and Harpending, Gathorne-Hardy and Harcourt-Smith 1994). assert that we have proposed a narrow hourglass shape for the bottleneck. They have glossed over the fact that we proposed that the Late Pleistocene population bottleneck was likely to have been the result of three climatic events spanning 11,500 vears, or 550 generations. These events comprise the six-year volcanic winter at 71 ka, the 1000-year instant ice age it apparently initiated, and the early last glacial maximum, oxygen isotope stage 4, from 68 to 59.5 ka (Ambrose, 1998a). In other words, the postulated bottleneck that began 71 ka may have endured for 9% of the time since the origin of modern humans. Rogers and Jorde (1995) have shown that a bottleneck lasting only one generation will leave no significant imprint on genetic diversity, and will be effectively invisible in genetic reconstructions of population history. Therefore a six-year volcanic winter may have caused a dramatic population crash, but could not itself have greatly affected the genetic structure of human populations.

Gathorne-Hardy and Harcourt-Smith expect to find well-documented widespread population extinctions at this time if the volcanic winter was as severe as is claimed. However, this expectation is unwarranted. The Ordovician super-eruption, which is of the same magnitude as Toba, was apparently not associated with any mass extinctions (Huff et al., 1992). By this standard, none should be expected for Toba, and none were claimed (Ambrose, 1998a; Rampino and Ambrose, 2000).

Bottlenecks of this age have rarely been documented in other species. However, in order to identify a population bottleneck, one must obtain a substantial number of gene sequences to conduct the pairwise nucleotide sequence difference (mismatch) analysis of population structure, or to determine if the species has a star-like phylogenetic branching pattern like that of humans (Gagneux et al., 1999). The only species for which we have such data is chimpanzees, and the eastern subspecies Pan troglodytes schweinfurthii does indeed show a population expansion in the core montane refugium area at around 67 ka (Goldberg, 1996). Until the nucleotide sequences of many individuals of many more species are analyzed, it is premature to claim that there is no supporting evidence for late Pleistocene bottlenecks in other species. No studies of large numbers of gene sequences of other species that have been analyzed in this way are cited by Gathorne-Hardy and Harcourt-Smith.

Human adaptability in the early Upper Pleistocene

The degree to which humans expressed the capacity for modern behavior prior to the last ice age is a subject of ongoing investigation and intensive debate in African archaeology (McBrearty and Brooks, 2000; Ambrose and Lorenz, 1990; Klein, 1999, 2000). During the last interglacial (128-74 ka), substantial steps were

taken toward modern patterns of symbolic behavior, and sophisticated technologies and adaptive strategies were in their initial stages of development. Indeed, this trend was apparently accelerating during the latter half of the last interglacial (Watts, 1999; Henshilwood et al., 2002). However, social strategies of macro-regional integration and cooperation, which are adaptive in unpredictable environments, seem to have been comparatively poorly developed in the last interglacial, and territorial defense rather than intergroup cooperation was apparently the norm (Ambrose and Lorenz, 1990). Harsh environmental conditions during the volcanic winter, instant ice age and early glacial isotope stage 4, are hypothesized to have selected strongly for an unprecedented degree of social cooperation and information exchange between individuals and groups over large areas (Ambrose, 1998a, 1998b, 2002, 2003). The forerunners of true microlithic blade-based industries, and longdistance movement of fine-grained stone tool raw materials, which reflects this information exchange system, first appeared during the beginning of the last ice age in both eastern and southern Africa (Ambrose, 2002). With this enhanced system of macro-regional strategic social cooperation and information sharing, early last glacial modern humans survived volcanic winter, the instant ice age and the early glacial maximum, albeit at very low population densities, which are evinced by the remarkable scarcity of archaeological sites of this period throughout Africa (Ambrose, 1998a). Soon after perfecting this modern human regional social integration system, and the sophisticated, specialized tool technologies it permitted (Ambrose, 2002), Africans apparently gained the ability to expand into risky environments within Africa, and into other continents, producing two colonization bottlenecks (Ambrose 2003).

Conclusions

Arguments of Gathorne-Hardy and Harcourt-Smith and others against the significance of the Toba super-eruption for abrupt, catastrophic climate change and population reduction, have provided the opportunity for a detailed reexamination and restatement of the main points of the hypothesis of Toba's relationship to the human population bottleneck, and to cultural developments. In summary:

- 1. Mounting geological evidence strongly suggests the eruption was significantly larger than previously estimated, and caused a millennium of the coldest temperatures of the Upper Pleistocene.
- 2. Numerous genetic studies suggest that the population bottleneck was real rather than "putative", and that it occurred during the first half of the last glacial period. Estimating the duration of this bottleneck is complex, but it was unlikely to have been shorter than 20 generations, and may have been longer than 500. Mass extinctions were not a feature of this event, nor of other explosive volcanic eruptions of comparable magnitude throughout Cenozoic history.
- 3. Capacities for modern human behavior were undoubtedly present during the last interglacial, but the stable environments of this period did not foster widespread adoption of the strategic cooperative skills necessary for survival in the last glacial era. Modern humans may have eventually developed such strategies during the last ice age, but they were crucial for survival when volcanic winter arrived. We are the descendants of the few small groups of tropical Africans who united in the face of adversity.

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