A brush fire feedback loop for the ramp-like rise in hominin brain size that began 2.4 million years ago

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During the first million years of the Pleistocene climate changes, our ancestors' brain size doubled. Enlargement continued at the same rate, suggesting a self-sustaining process with a rate-limiting component. For large grazing animals and their predator *Homo erectus*, I analyzed the brush-fire cycle behind grasslands' brushy frontier, seeking a feedback loop. The burn scar's new grass is an empty niche for grass-specialized herbivores, which evolved from mixed feeders only in the early Pleistocene. The frontier subpopulation of grazers discovering the auxiliary grassland quickly multiplies. Following this boom, a bust occurs several decades later when the brush returns; it squeezes this offshoot population back into the core grasslands population. For both prey and predators, such a feedback loop can shift the core's gene frequencies toward those of the brush explorers.

Hunters of both browsers and grazers spend more time in the brush than those specializing in grazers; this versatility becomes a candidate for differential amplification. Any brush-relevant allele could benefit from amplifying feedback by such trait hitchhiking, so long as its phenotypes also concentrate near where empty niches can open up in the brush for grazers and their predators. Increased versatility likely correlates with larger brain size on the evolutionary time scale. Among the tasks likely to need the shade of brush are toolmaking and food preparation. The more versatile, larger-than-average brains need only spend more-than-average time in the catchment zone for this recursive evolutionary process to keep average brain size increasing even further, making advance room for some future functionality in the cerebral cortex.

As the ice ages began 2.5 million years, Africa dried and the great savannas developed (1). Bursts of speciation promptly occurred among the herbivores (2). In their hominin predators, brain size began to increase and inexplicably doubled over the next million years (Fig. 1). Furthermore, brain size (3,4) kept on increasing at the same rate as the initial doubling, even without any additional increase in stature.

The uninflected ramp-like rise, seen when non-ancestral data points are excluded, suggests that the rate of enlargement is neither sensitive to such ice age trends as the progressively colder glacial temperatures (Fig. 1), nor to the major transitions in toolmaking complexity, nor to the appearance of successor *Homo* species. The brain's enlargement rate of 453 cm^3 myr^{-1} over 2.4 myr may simply reflect the rate-limiting step among even faster processes contributing to enlargement (much as the slowest supplier of parts limits the speed of an assembly line).

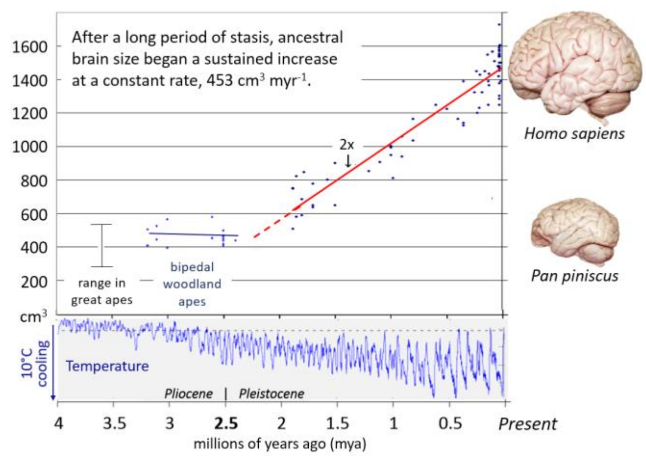

Fig. 1. The bipedal woodland apes had brains little larger than those of the great apes (bonobo is illustrated). Brain size in ancestral *Homo* doubled by 1.4 mya. The same enlargement rate continued until pre-agricultural *Homo sapiens*. The dashed line is extrapolated back from the solid line, a least squares fit to ancestral (to us) crania (N=68) between 15 kya and 1.9 mya. This excludes data points ftom known side branches: Neandertals, *Homo erectus* younger than 0.8 myr, and Australopiths younger than 2.4 mya. Earlier Australopiths (N=18) have a separate line fit. Data sets from (3,25; scaled photographs from T.W. Deacon.

For large grazing animals, I earlier analyzed (5) the brush-fire cycle behind grasslands' brushy frontier, seeking feedback loops. The burn scar's new grass is an empty niche for grass-specialized herbivores, which evolved from mixed feeders only in the early Pleistocene about 2.4 mya. The frontier subpopulation of grazers discovering an auxiliary grassland should quickly multiply.

Following this boom, a bust occurs several decades later when the brush returns; it squeezes this offshoot population back into the core grasslands population. For both prey and predators, such a feedback loop can shift the core's gene frequencies toward those of the brush explorers. Any brush-relevant allele could benefit from this amplifying feedback loop by trait hitchhiking (5), so long as its phenotypes concentrate near where empty niches can open up in the brush. Improved survival is unnecessary.

Such trait hitchhiking appears relevant to three of the central problems in evolution: (a) the doubling of our ancestors' brain size in the first million years of the Pleistocene; (b) promoting in *Homo* another of the rare instances of eusociality; and (c) bursts of evolutionary extravagance such as our higher intellectual functions. A feedback role in promoting antibiotic resistance is also postulated (5).

The grass road out of Africa

Early *Homo erectus* appeared on the East African scene by 1.9 mya, with a shoulder already adapted for throwing projectiles (6). Hunting and scavenging the large grazing animals, they appear to have followed a grass road north out of equatorial Africa, making it to Dmanisi, at 42°N between the Black Sea and the Caspian, by 1.8 mya. The habitat there was similar to the African savanna: grasses, arid conditions, and an abundance of large herbivores (7).

What took *Homo erectus* from the trade-wind tropics to a continental climate with harsh winters? One candidate for a process is that, when a herd of large grazing mammals has never encountered two-legged hunters before, they were easy prey. After being hunted a while, the herd becomes so wary that hunters move on to the next naïve herd. They cannot go back toward depleted and wary herds and so, like a burning fuse, they advance to the next hunter-naïve herd farther up the grass road whose northern terminus is the Arctic Ocean.

The border of the grass road may be a shoreline or a hyper-arid zone but the usual border is brush, providing occasional shade. It usually has a ragged edge, with narrowing paths of grass that terminate in a brushy dead end.

Brush as a part-time hominin habitat

The mile-high savannas of East Africa and South Africa have a particularly high rate of lightning strikes. Many brush fires result and, in the dry season, a large area can burn. Soon, grass sprouts. If the burn scar has a path connecting to inhabited grassland, grazing animals from the brush frontier subpopulation will move in.

Predators would have followed the grazing animals into the auxiliary grassland, many skimmed off of the predator population exploiting the brushy dead ends. They too will experience a population boom, though more slowly as the temporary grassland would, in the case of hominins, endure little more than two generations. They too will be squeezed out and many could join the core population.

The hunter-gatherer bands, originally attracted into the grass road by the succession of grazing herds, would have regularly visited the brush frontier, seeking shade and the traditional foods obtained by gathering. With long sticks, they could club small animals in the brush, including such small browsers as dik-dik. Cooking or overnight campfires, once invented perhaps 1.8 mya (8), would have required daily gathering of firewood behind the brush borders of grasslands.

These are among the reasons why much of the grasslands hominin population might want to visit the brush in a touch-and-go manner. However, those whose innate habitat preferences cause them to hang out longer in the brush (greater dwell time) would benefit reproductively when lightning strikes.

Waterhole predation

The last waterholes remaining in the dry season were likely those near a brush border (the surviving brush indicating sufficient soil moisture in prior dry seasons). Despite lions hiding in the brush (Fig. 2), grazing herds of zebra and wildebeest will pay an obligatory visit to such a waterhole every other day; browsers need not visit as often because of the water content of leaves.

Fig. 2. A lioness hiding in the brush begins an attack at a waterhole in Etosha National Park, Namibia. Before human intervention, Etosha's savannas and woodlands would burn about once per decade, clearing brush. Being specialized for grass, zebra and wildebeest must visit waterholes much more frequently than species getting much of their water from consuming leaves. Credit: Des & Jen Bartlett, National Geographic Creative.

A lion kill is often followed by a contest with scavengers over possession of the carcass; spotted hyenas can take a carcass away from small groups of lions (9). Power scavenging need not carry away the entire carcass; *Homo erectus* could have used a sharp edge and blunt dissection to amputate a hind limb quickly, leaving behind the fat-filled belly to ensure that the temporarily displaced lions do not follow when a hind limb is carried away.

Vanishing into nearby brush should make this power scavenging technique somewhat safer; also, a sturdy tree trunk may be required later. Clubbing with a long bone, in the manner of a baseball bat, can create a spiral fracture, allowing access to bone marrow without tools or hyena-strength jaws.

Given such a milieu, the components of the *Homo erectus* feedback loop are:

- a central grasslands population of *Homo* that mixes, though some are inclined to hang out in the brush more than others;

- an allele concentration from this habitat preference, and the tendency to skim off the brush population when the path to the new niche opens up;
- a population boom for this biased *Homo* population, because their surplus-to-requirements offspring can grow up to reproduce, and because their food resource, the grazer population, doubles even more quickly to maintain a surplus of high-quality food;
- leakage of this biased boom time population back into the central core when brush returns, shifting core and brush frontier gene frequencies; andrepeat with the next brush fire.

With the predators getting their own population boom by hanging out in the catchment zone for the boom of a major food source, hitchhiking is enabled for hominid traits that tend to concentrate in the catchment for reasons other than predation on grazers–say, the shade-seeking utilized in my previous article (5) to address eusociality's communal nursery aspect.

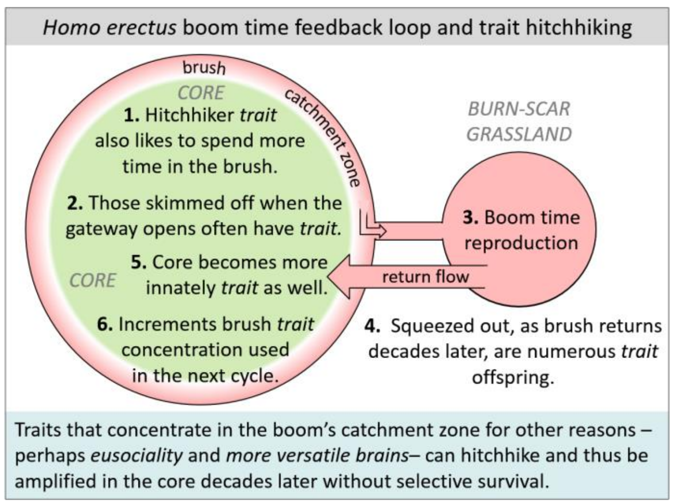

Fig. 3. The hominin population will secondarily experience a boom in the empty niche of the burn scar. Other genes with a concentration gradient between core and catchment zone, e.g., the more versatile hunter-scavengers and those clustering around cooperative nurseries in the brush's shade, will later shift their core gene frequencies via the feedback loop.

A hitchhiking bootstrap for brain enlargement

The amplifying feedback loop for grazers could have affected the genus *Homo* via promoting increasing behavioral versatility, and thus eventually brain size, provided that the more versatile had longer dwell times in the brush to concentrate the trait's allele there.

For example, those versatile enough to hunt both grazers and browsers would get more boom-time opportunities from the grazer boom, even though it is a boom only for grazers.

A long toolmaking session is best done in the shade provided by brush, as are advanced food preparation and cooperative nurseries. Those specializing in open-terrain confrontational scavenging (10), or running a herbivore to exhaustion (11), would often miss an opportunity to fill an empty niche opening up, back in the brush.

Building up behavioral versatility over the last 2.4 myr includes improving the hand-eye coordination for the “get set” ballistic movements (12, 13), such as accurate throwing from ever greater distances and the increasingly delicate hammering needed for the fine serrated cutting edges of Achulean-style tools. The new meat-rich diet exposed genes for both ballistic movements to improved survival.

Such elaborate (and often novel to the instance) muscle command sequences could, however, benefit from having a motor equivalent of working memory (14,15), a flexible workspace in the cerebral cortex for “get set” planning of ballistic movements, likely on the fringes of specialized movement areas. With time, a new innate movement specialization–say, hammering– could take root in the flexible workspace, though perhaps at the expense of losing some space for planning other ballistic movements, serving to decrease throwing accuracy.

However, there is a 15% spread in brain size in a given generation (16). Those individuals in a post-specialization generation, with a brain sufficiently larger than the current average, will have the original amount of flexible workspace despite the space commitment to the new specialization.

This “have your cake and eat it too” outcome might reasonably be called a preadaptation: mapping a second innovation is easier in those individuals of the current generation with sufficiently larger-than-the-current-average brains.

Because brain size is as heritable as parental height (16), bootstrapping to a new normal via assortative mating can be done by hanging out in the catchment zone for the boom time feedback loop, bypassing the need to keep proving the worth of a slightly bigger brain with each increment.

The constant rate of brain enlargement

Darwin's sexual selection (17) is what Fisher (18) called a "runaway" process. Female mate choice can directly shift the gene frequencies in the next generation; it need not use an external feedback loop through an empty niche to force the shift indirectly with boom-time numbers.

Fast feedback processes could, however, bootstrap both behavioral versatility and brain size. Other brain size considerations may be rate limiting: familiar candidates include staying ahead of the birth canal bottleneck (19) and that the brain's share of the blood supply had to keep increasing at the expense of something else, such as digestion (20).

Were some constraining genes lacking alternative versions, thus stopping enlargement, then 453 cm^3 myr^{-1} might be proportional to the rate at which cosmic rays or copying errors could create a new allele for amplification by the feedback loop–perhaps loosening a constraint on the faster underlying processes. A constant rate of mutation might then explain the linear rise in brain size.

As in chemistry's autocatalytic processes, this amplification loop has failure modes. Had grass-only herbivores been hunted to extinction, there would no longer have been boom times and amplification would have stopped–even though browsers and mixed-feeders continued to provide a meat diet for *Homo*. Once agriculture developed, the meat supply no longer constrained human population numbers.

Discussion

This identifies one fast autocatalytic process that could contribute to our ancestral brain's ramp-like enlargement. This feedback loop for the predators of grazers also suggests why ramp-like enlargement began 2.4 mya and not earlier (Fig. 1).

At 4 mya in East Africa, most large herbivores were unspecialized mixed feeders; by 2.4 mya, most had specialized for either grass or leaves (21). Although lightning strikes, brush fires, allele concentration in the catchment, and feedback loops could all operate before 2.4 mya, burn-scar booms for both grazers and their hominin predators could not operate, minimizing shifts in core allele ratios. Once grazer booms were enabled 2.4 mya, predator booms could begin to operate; only then did a free ride route became possible for some brush-related *Homo* traits, speeding the separation from Australopithecines.

A ramp mechanism facilitating trait hitchhiking for versatility does open up a new way of thinking about an evolutionary extravagance, such as the large gap in intellect between great apes and preagricultural humans that so puzzled Alfred Russel Wallace (22). Structured cognitive functions are extravagant by great ape standards and it is difficult to make selective survival arguments, especially for their early phases.

Hitchhiking now seems promising to explore as an alternative evolutionary path for syntax and the other higher intellectual functions: structured music, contingent planning, chains of logic, games with rules about possible moves, analogies that extend to parables, and creativity's eureka moments when incoherent mental assemblies become coherent fits, good to go.

If a projectile misses, dinner tends to run away. I have suggested that projectile predation regularly rewarded improvements in the structured planning needed for novel ballistic movements, incidentally improving the neural circuitry also utilized by the higher intellectual functions (13,14,23).

For exploring their evolution, examining settings may be more productive than the usual focus on increments in usefulness. Any trait with alleles that concentrate in the catchment zone may be on a fast track. For example, pantomime or short-sentence protolanguage can be used to gossip about “Who did what to whom, where, when, and with what means?” (Given the instincts guiding female mate choice, reputation is often of interest.) But a speedier verbal version needs some help from structuring conventions (grammar and syntax) if a listener is to quickly understand the longer or more complex expressions.

For the shade of the catchment zone, hands are often busy and so the verbal structured version of gossip may get many hours of practice each day (24) and would be routinely overheard by young children. While there is little in this language example that is exposed to selective survival, the shady setting provides preferred access to selective fecundity’s (5) boom time loop.

As sexual selection did for the extravagant peacock tail, feedback loops can surprise us with progressions that keep going automatically–as in that afore-mentioned preadaptation for the next new thing, in all the children who are above average.

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References

1. deMenocal PB. African climate change and faunal evolution during the Pliocene-Pleistocene. Earth and Planetary Science Letters. 2004; 220: 3-24. Link: www.ldeo.columbia.edu/~peter/site/Papers_files/deMenocal.2004.pdf.

2. Vrba ES. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In Vrba ES, Denton GH, Partridge TC, Burckle LS, editors. Paleoclimate and Evolution with emphasis on Human Origins. New Haven CT: Yale University Press; 1995, pp. 385-424.

3. Holloway RS, Yuan MS, Broadfield DC. The Human Fossil Record: Brain Endocasts - The Paleoneurological Evidence, Volume Three. New York: Wiley; 2004, Appendix 1, p. 295. Fig. 1 (upper) is edited down from their database.

4. Shultz S, Nelson E, Dunbar RIM (2012). Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. Philosophical Transactions of the Royal Society B: Biological Sciences. 2012; 367(1599): 2130-2140. DOI: 10.1098/rstb.2012.0115.

5. Calvin WH. Eusociality and other improbable evolutionary outcomes can be accelerated by trait hitchhiking in boom-bust feedback loops. Preprint. Available: bioRxiv 2016; doi: http://dx.doi.org/10.1101/053819

6. Roach NT, Venkadesan M, Rainbow MJ, Lieberman DE. Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo*. Nature 2013; 498: 483–486. doi: 10.1038/nature12267.

7. Messager E, Lordkipanidze D, Kvavadze E, Ferring CR, Voinchet P. Palaeoenvironmental reconstruction of Dmanisi site (Georgia) based on palaeobotanical data. Quaternary International 2010; 223: 20–27. doi: 10.1016/j.quaint.2009.12.016.

8. Gowlett JAJ, Wrangham RW. Earliest fire in Africa: towards the convergence of archaeological evidence and the cooking hypothesis. Azania 2013; 48: 5-30. doi: 10.1080/0067270X.2012.756754.

9. Trinkel M, Kastberger G. Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. African Journal of Ecology 2005; 43: 220–224. doi: 10.1111/j.1365-2028.2005.00574.x.

10. Bunn HT. Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene Homo. In: Stanford CB, Bunn HT, editors, Meat-eating and Human Evolution, pp. 199-218. New York: Oxford University Press; 2001.

11. Lieberman DE, Bramble DM, Raichlen RA, Shea JJ. Brains, brawn, and the evolution of human endurance running capabilities. Grine FE, Fleagle JG, Leakey RE, editors. The First Humans – Origin and Early Evolution of the Genus *Homo*. Amsterdam: Springer Netherlands; pp. 77-92; 2009. Link: link.springer.com/chapter/10.1007%2F978-1-4020-9980-9_8.

12. Calvin WH. A stone's throw and its launch window: timing precision and its implications for language and hominid brains. Journal of Theoretical Biology 1983; 104: 121-135. Link: cogprints.org/21/1/1983JTheoretBiol.htm

13. Calvin WH. A Brain for All Seasons: Human Evolution and Abrupt Climate Change. London and Chicago: University of Chicago Press; 2002.

14. Calvin WH. A Brief History of the Mind. New York: Oxford University Press; 2004.

15. Gallivan JP, Johnsrude IS, Flanagan JR. Planning ahead: object-directed sequential actions decoded from human frontoparietal and occipitotemporal networks. Cerebral Cortex; 2015. doi: 10.1093/cercor/bhu302.

16. Witelson SF, Beresh H, Kigar DL. Intelligence and brain size in 100 postmortem brains: sex, lateralization and age factors. Brain 2006; 129: 386–398. doi: 10.1093/brain/awh696.

17. Darwin CR. The Descent of Man, and Selection in Relation to Sex. London: John Murray; 1871.

18. Fisher RA. The Genetical Theory of Natural Selection. Oxford: Clarendon; 1930. Link: jhered.oxfordjournals.org/content/21/8/349.

19. Huseynov A, Zollikofer CP, Coudyzer W, Gascho D, Kellenberger C, Hinzpeter R, Ponce de León MS. Developmental evidence for obstetric adaptation of the human female pelvis. Proc Natl Acad Sci U S A. 2016; 113(19): 5227-32. doi: 10.1073/pnas.1517085113.

20. Aiello LC, Wheeler P. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. Current Anthropology 1995; 36: 199-221. Link: www.jstor.org/stable/2744104.

21. Cerling TE, Andanje SA, Blumenthal SA, Brown FH, Chritz KL, Harris JM, et al. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. Proc Natl Acad Sci U S A. 2015; 112: 11467-11472. doi: 10.1073/pnas.1513075112

22. Bickerton D. More than Nature Needs: Language, Mind, and Evolution. Cambridge MA: Harvard University Press; 2014.

23. Calvin WH, Bickerton D. Lingua ex Machina. Cambridge MA: MIT Press, p.83; 2000.

24. Dunbar RIM. Gossip in evolutionary perspective. Review of general psychology 2004; 8: 100-110. doi: 10.1037/1089-2680.8.2.100.

25. Lisiecki LE, Raymo ME. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. Paleoceanography 2005; 20: PA1003. doi: 10.1029/2004PA001071. Fig. 1 (lower) is replotted from their database.