Reply to Fontes-Villalba et al.: On a reluctance to conjecture about animal food consumption

Fontes-Villalba et al. (1) correctly observe that carbon isotope ratios in tooth enamel do not speak directly to plant versus animal food ingestion. Carbon isotope ratio data are useful for quantifying the consumption of C_3- or C_4-derived carbon, whether it comes directly from C_3 or C_4 plants or indirectly through consumption of animals that eat those plants. Not only do we acknowledge as much in our recent series of papers, but we have made this point in print many times over the past two decades (ref. 2 and references therein).

However, to what extent can we speak to animal food consumption by early hominins? To address this question, we first note that "early hominin diet" is a convenient abstraction at best, as the hominins discussed in our reports spanned a period of greater than 3 million y, and evinced major differences in masticatory anatomy and associated archaeology. Given this heterogeneity, and the likely corollary of marked diversity in early hominin diets, it is not only plausible—but probable—that C_4 food acquisition and consumption differed among hominin species.

For example, given *Paranthropus boisei*'s high $\delta^{13}C$ values, robust mandibles, low-cusped cheek teeth, and diminutive incisors and canines, it is improbable that its major C_4 dietary input was meat. Indeed, even savanna carnivores may not attain such high $\delta^{13}C$ values (3). It is, therefore, most parsimonious to ascribe the preponderance of its C_4 "signal" to the direct consumption of C_4 plant foods.

The situation for contemporaneous *Homo* might well be different. Its dental morphology, the general belief that it made and wielded stone tools, and arguments derived from energetics are consistent with *Homo* having consumed greater amounts of animal protein. Nevertheless, these lines of evidence tell us little about the abundance of animal products consumed. For example, although the archaeological record unquestionably informs us about the technical capacities of early hominins, it cannot discriminate between diets that comprise 5% or 50% animal foods. In addition, the "expensive tissue hypothesis" cited by Fontes-Villalba et al. (1) does not speak directly to animal food consumption, but rather to an increase in the consumption of "high-quality" (i.e., nutritionally dense) foods by *Homo*. These foods include not only animal tissues, but also "nuts or underground tubers" (4).

We are reluctant to speculate about the fatty acid and micronutrient requirements of early hominins and their dietary implications. We simply note that most primates, including some modern humans, flourish on diets that are dominated by plant foods. Indeed, among extant catarrhine primates it is only modern humans with a technologically sophisticated hunting armamentarium that have been documented to subsist (under certain conditions) on large amounts of animal flesh (5).

We agree with Fontes-Villalba et al. (1) that it would be surprising if most early hominins did not consume animal foods to some extent, given our knowledge of the diets of our closest kin (*Pan* spp.) and the observed behavior of other savanna primates (6). We caution, however, that it is not possible at present to meaningfully address the relative importance of faunivory for any Pliocene or early Pleistocene hominin species, including those attributed to the genus *Homo*. It is for this reason that we eschewed conjecture about animal food consumption in the 11 or so taxa discussed in our papers.

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Author contributions: M.S., Z.A., T.E.C., F.E.G., W.H.K., M.G.L., J.A.L.-T., F.K.M., K.E.R., B.A.W., and J.G.W. designed research; M.S., Z.A., T.E.C., F.E.G., W.H.K., M.G.L., J.A.L.-T., F.K.M., K.E.R., B.A.W., and J.G.W. performed research; M.S., Z.A., T.E.C., F.E.G., W.H.K., M.G.L., J.A.L.-T., F.K.M., K.E.R., B.A.W., and J.G.W. analyzed data; and M.S., Z.A., T.E.C., F.E.G., W.H.K., M.G.L., J.A.L.-T., F.K.M., K.E.R., B.A.W., and J.G.W. wrote the paper.

The authors declare no conflict of interest.

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www.pnas.org/cgi/doi/10.1073/pnas.1314368110