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1 **Mineral contributions to the diet and health of wild chimpanzees in three**  
2 **East African forests, with notes on mechanisms and underlying mineral con-**  
3 **centrations**

4  
5 Running title: Mineral contributions to chimpanzee diet

6  
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14 land

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3 17 **Abstract**  
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5 18 We present new data on the ingestion of minerals from termite mound soil (TMS) by chim-  
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7 19 panzees (*Pan troglodytes schweinfurthii*) living in the Budongo Forest Reserve, Uganda.

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10 20 Termite mound soil is here shown to be a rich source of minerals, containing high concen-  
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12 21 trations of iron and aluminium. Termite mound soil is not, however, a source of sodium. The  
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14 22 concentrations of iron and aluminium are the highest yet found in any of the mineral  
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16 23 sources consumed. Levels of manganese and copper, though not so high as for iron and al-  
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18 24 uminium, are also higher than in other dietary sources. We focus on the contribution of  
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20 25 termite mound soil to other known sources of mineral elements consumed by these apes,  
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22 26 and compare the mineral content of termite soil with that of control forest soil, decaying  
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24 27 wood, clay, and the normal plant-based chimpanzee diet at Budongo. Samples obtained  
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26 28 from Mahale Mountains National Park and Gombe National Park, both in Tanzania, show  
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28 29 similar mineral distribution across sources. Finally, we suggest three distinct but related  
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30 30 mechanisms by which minerals may come to be concentrated in the above-mentioned  
31  
32 31 sources.  
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39 33 **Keywords:** geophagy; *Pan troglodytes*; termite mound soil, minerals; diet; chimpanzees;  
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41 34 Uganda; Tanzania  
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3 **35 Introduction**  
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6 36 Some bird and mammalian species, including elephants, macaques, tamarins, gorillas, chim-  
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8 37 panzees and humans (Wilson 2003), consume soil of a variety of kinds, often in the form of  
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10 38 clay, for its mineralogical content. In doing so they obtaining both essential minerals, which  
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12 39 may have nutritional value, and non-nutritional minerals that can aid in the detoxification of  
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14 40 harmful compounds such as alkaloids in the diet (Klaus. Klaus-Hugi and Schmid, 1998), and  
15  
16 41 alleviate gastro-intestinal upsets (Mahaney et al., 1996). As pointed out by Wilson (2003), in  
17  
18 42 a review of the literature in this field, physiological tests are needed to determine bioavaila-  
19  
20 43 bility of mineral elements eaten in the course of geophagy. Probably no single characteristic  
21  
22 44 of soils eaten by animals and humans can account for their consumption (Abrahams, 1999;  
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24 45 Wilson, 2003), with mineral supplementation, medical, and detoxification functions all play-  
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26 46 ing a part (Aufreiter, Hancock, Mahaney, Strambolic-Robb and Sanmagudas, 1997; Aufreiter  
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28 47 et al., 2001; Ketch, Malloch, Mahaney and Huffman, 2001; Mahaney, 1993; Mahaney et al.,  
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30 48 1999; Vermeer and Ferrell, 1985; Wilson, 2003).  
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38 50 The normal diet of wild chimpanzees in the Budongo Forest, Uganda, is typical of East Afri-  
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40 51 can chimpanzee groups, and consists primarily of fruits and leaves, with additional flowers,  
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42 52 bark, and pith. Besides these plant-based items, meat and insects are eaten sporadically  
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44 53 when they become available. Both meat, obtained primarily by killing monkeys (Nishida,  
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46 54 Uehara and Nyundo, 1979; Goodall, 1986; Mitani and Watts, 2001; Newton-Fisher, Notman  
47  
48 55 and Reynolds, 2002) and insects, for example termites (O'Malley and Power 2014), are high-  
49  
50 56 ly nutritious sources of minerals as well as proteins, fats and other dietary requirements.  
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53 57 However the bulk of the food eaten by wild chimpanzees is plant-based and this constitutes  
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55 58 80% or more of the daily diet of most individuals. While high in some minerals e.g. potassi-  
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3 59 um and calcium, the Budongo chimpanzees' diet lacks (or has low quantities) of others e.g.  
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5 60 aluminium, copper, manganese, and sodium, and, as a result, they need to locate these  
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7 61 minerals from other sources (Reynolds, Lloyd, Babweteera and English, 2009). Earlier work  
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9 62 (Reynolds et al., 2009; Reynolds, Lloyd and English, 2012; Reynolds et al., 2015) explored a  
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11 63 number of dietary supplements for mineral acquisition, namely decaying pith of *Raphia fa-*  
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13 64 *rinifera* and the decaying wood of *Cleistopholis patens*, which provide appreciable amounts  
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15 65 of sodium (Reynolds et al., 2009, 2012), and clay, which provides substantial amounts of  
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17 66 iron (Reynolds et al., 2015). In this paper we show that termite mound soil is a further valu-  
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19 67 able source of minerals eaten by chimpanzees in the Budongo Forest Reserve, Uganda, by  
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21 68 the Kasekela group at Gombe National Park and by the M group at the Mahale Mountains  
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23 69 National Park (Aufreiter et al., 2001).  
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28 70 Some discussion revolves around the extent of bioavailability of the iron ingested in termite  
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30 71 mound soil (Aufreiter et al., 2001). In part this resolves itself into the question of whether  
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32 72 the iron is in ferric ( $\text{Fe}^{3+}$ ) or ferrous ( $\text{Fe}^{2+}$ ) form. If the former, it is not bioavailable; if the lat-  
33  
34 73 ter it is. Experimental work (Aufreiter et al., 2001) using a medium with low pH to simulate  
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36 74 digestive conditions suggests that most of the iron in soil is in ferric form and only a small  
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38 75 part is ferrous. This finding suggests that the nutritional value of ingested termite mound  
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40 76 soil may be limited. However we should note that in humans a ferric reductase enzyme, du-  
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42 77 odenal cytochrome B, reduces ferric  $\text{Fe}^{3+}$  to  $\text{Fe}^{2+}$  (McKie et al., 2001). This enzyme, if present  
43  
44 78 in chimpanzees, as seems likely, serves to increase the bioavailability of iron ingested in  
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46 79 termite mound soil. If present, ferrihydrite, a hydrous ferric oxide mineral, is likely to be sol-  
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48 80 ubilised (Wilson, 2003). Mahaney et al (1997) concluded that in geophagy soils eaten by  
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50 81 chimpanzees in the Kibale Forest, Uganda, 20% of ingested iron was bioavailable, sufficient  
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52 82 for nutritional significance. In a study of soils eaten by humans and sold in local markets in  
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3 83 Uganda, it was concluded that consumption of 5g of soil contributed 19-25% of daily needs  
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5 84 for iron (Abrahams and Parsons, 1997; Abrahams 1997). Geissler et al. (1998), by contrast,  
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7 85 found that despite consuming 30g daily of iron-rich termite mound soil, anaemia remained  
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9 86 prevalent in a human population in Kenya. Pregnant women were particularly prone to eat-  
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11 87 ing clays in Uganda and other tropical countries. Pregnant Chacma baboons (*Papio ursinus*)  
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13 88 spent more time consuming iron-rich clay at monitored geophagy sites in Western Cape,  
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15 89 South Africa than baboons of other age-sex classes (Pebsworth, Bardi and Huffman, 2011).  
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21 91 Whereas the majority of minerals discussed in this paper can be regarded as either major  
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23 92 minerals essential for life or minor minerals required only as trace elements, aluminium is  
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25 93 neither of these and is not essential for life. Its ingestion in termite mound soil, probably in  
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27 94 the form of kaolinite (Johns and Duquette, 1991; Mahaney et al., 1995) and in some cases  
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29 95 gibbsite (Bolton, Campbell and Burton, 1998), probably serves medicinal functions, by re-  
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31 96 ducing acidity in the gut and neutralising plant toxins such as condensed tannins (Hladik,  
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33 97 1977; Goodall, 1986). Condensed tannins are ingested by chimpanzees on a daily basis at  
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35 98 Budongo, being found at high concentrations in several species of figs (*Ficus sp*), particularly  
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37 99 in the seed component. One fig species with a high concentration of condensed tannins, *Fi-*  
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39 100 *cus sur*, is the second most frequently eaten food of the Budongo chimpanzees. Condensed  
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41 101 tannins thus appear to be well tolerated by chimpanzees (Reynolds, Plumtre, Greenham and  
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43 102 Harbone, 1998; Wrangham, 1993; Aufreiter et al., 2001).  
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51 104 Termite mound soil eating appears to be an opportunist and largely individual activity, oc-  
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53 105 ccurring when the animals pass by a termite mound in the forest, often moving from one  
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55 106 vegetative feeding site to another. Observations by researchers and field assistants indicate  
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3 107 that “Gombe chimpanzees eat termite mound soil, on average, once a day” (Wrangham,  
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5 108 1977) and the same may be true at Mahale and Budongo. Anecdotal reports suggest that at  
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7 109 all three sites termite mound soil eating is more frequent among females than males, but  
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9 110 quantitative data are lacking. Termite mounds present a hard surface (Figure 1) and chim-  
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12 111 panzees either bite off a piece with their teeth or break off a piece with their fingers (Figure  
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14 112 2). At Mahale, chimpanzees eat the soil of termite mounds through the year, possibly to as-  
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16 113 sess the reproductive condition of the termites (Uehara, 1982), as well as during times of  
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18 114 gastrointestinal distress. At Gombe, about once a day, as they pass termite mounds, chim-  
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20 115 panzees pick off and eat a “walnut” sized piece of termite mound soil (Goodall, 1986; Ma-  
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22 116 haney, Hancock, Aufreiter and Huffman, 1996; Huffman, 1997). Time spent feeding on ter-  
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24 117 mite mound soil is short: at Gombe, 32 bouts of geophagy were measured and the mean  
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26 118 duration was 1.7 min, range 1-8 min (data from Wrangham, 1977; quoted in Uehara,  
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28 119 1982:53). Co-feeding in large groups on termite mound soil, seen for example when feeding  
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30 120 on other soils such as clay, has not been observed. And, unlike clay, termite mound soil is  
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32 121 not eaten with leaves. At Budongo, if termites are present in termite mound soil, they are  
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34 122 also eaten (Newton-Fisher, 1999), but use of tools for termite fishing has not been observed  
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36 123 at Budongo, possibly because termite mounds of *Pseudacanthotermes* are less fishable, hav-  
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38 124 ing few or no external holes (Collins & McGrew, 1985), unlike those of *Macrotermes* species.  
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40 125 At Mahale, use of tools for termite fishing by the M group has only been seen occasionally  
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42 126 (Takahata, 1982); while at Gombe, chimpanzees termite fish year around, though concen-  
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44 127 trate this activity around the wet months (Goodall, 1986; Uehara, 1982). Goodall (1986:256)  
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46 128 also refers to Wrangham’s 1977 study at Gombe: “Analysis of samples of termite clay ... re-  
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48 129 vealed substantial quantities of potassium, magnesium and calcium and traces of copper,  
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3 130 manganese, zinc, and sodium ... feeding on termite clay may be to neutralise tannins and  
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5 131 other poisons present in plant foods (Hladik, 1977)".  
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7 132 In this paper we explore the concentrations of mineral elements in termite mound soil  
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9 133 across three sites, as compared to control soil samples and other dietary sources. We go on  
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11 134 to provide possible explanations for the mechanisms by which mineral elements are con-  
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13 135 centrated in different soil and plant-based sources.  
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## 21 138 **Methods**

### 23 139 **Subjects and sites**

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26 140 Data were collected in the Budongo Forest Reserve, in north-western Uganda; and the  
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28 141 Gombe National Park and the Mahale Mountains National Park, both in western Tanzania.  
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30 142 Subjects at each of the three sites sampled were all wild East African chimpanzees (*Pan*  
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32 143 *trogodytes schweinfurthii*). Males and females of all age groups, except infants (aged 0-5  
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34 144 years old) were seen eating at the termite mounds from which samples were collected.  
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36 145 Samples described here were collected between July 2015 and October 2017. Termite spe-  
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38 146 cies are shown in Table 1.  
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### 44 148 **Soil sample collection**

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47 149 Across sites, termite mound soil samples were collected by removing a 10-15g piece of  
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49 150 mound soil from a termite mound, using a sterile knife. Clean gloves were worn to prevent  
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51 151 contamination from human sweat. In addition, control samples were collected of forest soil.  
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53 152 At Budongo, control samples were taken from forest soil 1-3m laterally from the termite  
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55 153 mound and 15-20cm deep. At Gombe control samples were taken from forest soil 1m later-

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3 154 ally from the termite mound and 15-20cm deep. Control samples were not collected at Ma-  
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5 155 hale. All samples were put into individual new plastic bags, marked with date, collector,  
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7 156 block number (an indication of location within the chimpanzee territory), and sample num-  
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9 157 ber, and taken back to base camp where they were dried at a temperature of 40° C until ful-  
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11 158 ly dry. Five grams of each dried sample was then transferred to new sterile plastic container  
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14 159 tubes for onward shipment to the UK.  
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### 19 161 **Laboratory Analysis of Soil Samples**

21 162 The soil samples were dried to constant weight in an oven at 105°C for 6 hours. The total  
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23 163 mass of the dried material was determined. Duplicate samples were prepared by taking 0.1g  
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25 164 of the material and 3ml of Aqua Regia in a 10ml centrifuge tube. The samples were digested  
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27 165 in a water bath at 85°C for 3 hours. 7ml of ultrapure Type 1 water was then added to each  
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29 166 sample and the samples mixed using a vortex mixer. A 1ml aliquot of each sample was dilut-  
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31 167 ed 10 fold with Type 1 water for analysis. The elemental content of each sample was then  
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33 168 determined using a Perkin Elmer Optima 2100 DV Inductively Coupled Plasma Optical Emis-  
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35 169 sion Spectrometer (ICP-OES). Standards and a blank were made up at 2, 4, 6, 8 and 10 ppm  
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37 170 concentrations with 3% HNO<sub>3</sub> and three replicates of each element were measured. Each  
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39 171 sample was analysed in triplicate and the average of the triplicate analysis taken for each  
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41 172 duplicate. The mean of the duplicate analyses of the individual soil samples was then taken  
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43 173 to be representative of that soil sample. The elemental content per kg of dried material was  
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45 174 calculated from the raw data.  
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### 54 176 **Statistical analyses**

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3 177 The data for each variable were tested for normality of distributions and equality of error  
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5 178 variances. Where these assumptions were not upheld non-parametric tests were used. Re-  
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7 179 sults were considered significant at  $\alpha=0.05$ . All data were analysed using SPSS v24.  
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## 13 14 15 182 **Results**

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18 183 Values are mg/kg except where otherwise stated. We found a wide variation in the concen-  
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20 184 tration of the mineral elements measured in termite mound and control soil samples (Table  
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22 185 2). Iron, aluminium, and potassium were the highest in both termite mound soil and control  
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24 186 samples across sites. Zinc, sodium and copper had the lowest concentrations in both soil  
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26 187 types (with the exception of Mahale where zinc was more abundant in termite mound soil,  
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29 188 see Table 2).  
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## 32 33 34 190 **Budongo**

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36 191 Potassium, phosphorus, aluminium, and copper were all more concentrated in termite  
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38 192 mound soil than in control soil; no other minerals varied in their abundance between soil  
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40 193 types (Table 2). When compared with mineral concentration in the normal diet (data taken  
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42 194 from Reynolds et al., [2012](#), Table 3), potassium (Kruskal Wallis:  $X^2= 0.95$   $p=0.329$ ) and phos-  
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44 195 phorus (Kruskal Wallis:  $X^2= 0.80$   $p=0.373$ ) are found at similar concentrations in termite  
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46 196 mound soil. Concentrations of all other minerals measured differed. Termite mound soil had  
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48 197 concentrations of iron over 75 times higher ( $49.1 \pm 19.6$  g/kg,  $n=39$ ) than found in the nor-  
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50 198 mal diet ( $649 \pm 1309$  mg/kg,  $n=24$ ; Kruskal Wallis:  $X^2= 44.1$   $p<0.001$ ); and a very large con-  
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52 199 centration of aluminium (termite mound soil  $15,300 \pm 4690$  mg/kg,  $n=39$ ), which is com-  
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3 200 pletely absent from the normal diet (n=24; Kruskal Wallis:  $X^2= 46.4$  p<0.001). Of other min-  
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5 201 erals, calcium ( $X^2= 9.09$  p=0.003), magnesium ( $X^2= 5.13$  p=0.024) and sodium ( $X^2= 44.1$   
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7 202 p<0.001) were higher in the normal diet, while manganese ( $X^2= 43.9$  p<0.001) and copper  
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9 203 ( $X^2= 18.6$  p<0.001) were higher in termite mound soil.  
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#### 14 205 **Gombe**

16 206 As at Budongo, iron had the highest concentrations in both termite mound soil and control  
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18 207 samples from Gombe, followed by aluminium (see Table 2). Levels of magnesium were  
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20 208 higher across Gombe soil samples (n=19) than in Budongo soil samples (n=66; Mann-  
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22 209 Whitney: U=71, p<0.001); with concentrations in termite mound soil over 5 times higher in  
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24 210 Gombe (Table 2; Mann-Whitney: U=22, p<0.001). As at Budongo zinc, sodium and copper  
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26 211 had the lowest concentrations. Sodium was completely absent from termite mound soil at  
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28 212 Gombe, but was present in small amounts in control samples. So, as at Budongo, Gombe  
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30 213 termite mound soil provided the high concentrations of iron and aluminium, together with  
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32 214 some magnesium and other minerals, with the notable exception of sodium. Concentrations  
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34 215 of potassium, iron, aluminium, and copper were all higher in termite mound than in control  
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36 216 soil samples at Gombe; concentrations of sodium and sulphur were lower (Table 2).  
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#### 44 218 **Mahale**

46 219 As at Budongo and Gombe, iron and aluminium were present in the highest concentrations,  
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48 220 although at Mahale aluminium, rather than iron, was highest; at almost double the concen-  
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50 221 trations present in Budongo or Gombe (Table 2; Kruskal-Wallis:  $X^2= 25.13$ ; p<0.001). Also as  
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52 222 at Budongo and Gombe, sodium and copper had the lowest concentrations at Mahale. None  
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3 223 of the three sites compared had a consistently higher or lower overall concentration of min-  
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5 224 erals in any particular soil type.  
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10 226 **Comparisons between termite mound soil, clay, decaying wood, and the normal diet of**  
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12 227 **fruit and leaves at Budongo**  
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14 228 We compare the mineral content in termite mound soil with that present in clay (data from  
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16 229 Reynolds et al 2015, Table 3), decaying wood (*Raphia farinifera* and *Cleistopholis patens*)  
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18 230 (data from Reynolds et al., Tables 1 and 2 combined), and the normal diet of fruit and leaves  
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20 231 at Budongo (data from Reynolds et al., 2012, Table 3). The differences between means  
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22 232 shown in Table 3 are significant for all minerals shown.  
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30 235 **Discussion**  
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33 236 Given the distance between the three sites (Budongo to Gombe 740km, Gombe to Mahale  
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35 237 180 km) there is a high degree of similarity in the concentration of soil minerals between  
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37 238 them. Termite mound soil provides chimpanzees with iron (Fig 3) and aluminium (Fig 4) in  
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39 239 high concentrations at all three, with provision of other essential minerals at lower concen-  
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41 240 trations at all of them, and absence or near absence of sodium at them all. Thus, a clear pic-  
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43 241 ture emerges of the contribution of termite mound soil to the mineral intake of chimpan-  
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45 242 zees in East Africa and possibly elsewhere.  
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51 244 Similar differences between termite mound soil and control samples have been found by  
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53 245 Adams et al. (2017), Mahaney et al. (1996, 1999), Aufreiter et al. (2001), Sarcinelli et al.  
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55 246 (2009). This widespread difference indicates a process whereby some mineral elements be-  
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3 247 come concentrated in termite mound soil. What is the process? It could take place at the  
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5 248 stage of acquisition of soil by termites, which involves a prolonged process of embedding  
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7 249 grains of soil in ingested water and salivary secretions (Turner, 2005) after which they are  
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9 250 carried up into the mound to the building point. However, minerals that are relatively scarce  
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11 251 in control forest soil are also relatively scarce in termite mound soil. Sodium in particular,  
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13 252 scarce in forest soil, is very low or absent (i.e. below measurement detection limits) in ter-  
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15 253 mite mound soil (see also Tweheyo et al., 2006). The main process whereby minerals be-  
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17 254 come concentrated in termite mound soil is therefore unlikely to be selection by termites.  
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23 256 Low values (or absence) of sodium in termite mound soil were found in the initial samples of  
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25 257 termite mound soil collected as part of a study of minerals in clay (n=5; Reynolds et al.,  
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27 258 2015). This finding is now validated by a larger sample size across three different sites. The  
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29 259 complete absence of sodium from termite mound soil at Gombe, while present in control  
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31 260 samples, could indicate avoidance or rejection of sodium by termites or that they consume  
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33 261 sodium for their own requirements. The latter may be the correct explanation. Kaspari et al.  
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35 262 (2009, 2014) showed experimentally that numbers of termites in the soil and litter decom-  
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37 263 position rates were higher in Amazonian forest plots to which sodium had been applied than  
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39 264 in control plots. Whether sodium consumption is a common attribute of termites or can ex-  
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41 265 plain the relative lack of sodium in Gombe termite mound soil is not known (Scheffrahn  
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43 266 pers. comm.).  
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51 268 High values of aluminium and iron and low values of sodium were also found by Mahaney et  
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53 269 al. (1996, 1997, 1999) and Tweheyo et al. (2006) who emphasised the possible medicinal  
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55 270 use of aluminium in clay in the form of metahalloysite. Metahalloysite has the same formula  
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3 271 as kaolinite,  $\text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4$  (Brindley, Robinson and MacEwan, 1946) and is used by humans  
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5 272 (commercially in the form of Kaopectate) to treat gastro-intestinal complaints (Hunter,  
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7 273 1973; Mahaney et al., 1997, 1999; Johns and Duquette, 1991; Wilson, 2003; Fairhead, 2016).  
8  
9 274 Smectite and gibbsite are further possible contributors to the efficacy of termite mound soil  
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11 275 (Wilson, 2003). Higher concentrations of mineral elements in termite mound soil than in  
12  
13 276 surrounding control soil were found by Aufreiter et al. (2001) and Adams et al. (2017) in a  
14  
15 277 study of arboreal termitaria in Peru.  
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### 21 279 **Mineral accretion**

22  
23 280 It is of great interest that chimpanzees appear to have discovered these three “hidden”  
24  
25 281 sources of minerals: plant-based, soil-based, and animal-generated. In two of the three  
26  
27 282 (plant-based and animal-generated) mineral concentration comes about as a result of water  
28  
29 283 evaporation. In each case, water containing minerals is drawn up in decaying wood by capil-  
30  
31 284 lary action, in the case of termite mounds transported by termites. In the third case, clay,  
32  
33 285 low levels of minerals occur in the forest substrate and these are leached out of the soil by  
34  
35 286 rain-water that collects in holes under trees.  
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41 288 At *Raphia farinifera* and *Cleistopholis patens* sites, chimpanzees chew the fibrous, decaying  
42  
43 289 wood containing minerals left behind after evaporation, following which they spit out  
44  
45 290 ‘wedges’ of fibrous matter. At clay sites it appears that the minerals are ingested by chim-  
46  
47 291 panzees by chewing the clay when it is in semi-solid form, or extracting it from clay-water  
48  
49 292 with the use of leaf or moss sponges (Reynolds et al., 2015). At termite mound soil sites,  
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51 293 chimpanzees chew pieces of mound soil in a similar way to the way they chew clay.  
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3 294 In each of the above cases, a low level of minerals exists in the environment, too dispersed  
4  
5 295 and at concentrations too low for detection and acquisition by large mammals such as  
6  
7 296 chimpanzees. Concentration of minerals may come about in three ways:

9  
10 297 (a) In the case of decaying *Raphia farinifera* palms, and *Cleistopholis patens* trees, these  
11  
12 298 are located in swamp forest which periodically floods, bringing in river water which  
13  
14 299 contains low levels of mineral elements leached from the soil and rocks along its  
15  
16 300 course. These elements are in low concentration (Reynolds et al., 2009, 2012, 2015).  
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18 301  
19  
20 302 swamp water upwards inside the tree's vertical, fibrous, pith-filled trunk. Because  
21  
22 303 the head of the *Raphia* palm has previously fallen off after the tree fruited, the top  
23  
24 304 of the trunk is now open and the whole trunk forms a cylinder filled with fibrous  
25  
26 305 pith. Water containing low levels of minerals can enter this cylinder from below and  
27  
28 306 rises up the fibres. As water evaporates from the top of the cylinder, it will leave its  
29  
30 307 mineral content behind. As a result we speculate that this becomes concentrated,  
31  
32 308 and it is this source that the chimpanzees have learned to access by making a hole in  
33  
34 309 the bark of the lower trunk (see Reynolds et al., 2009). In the case of *Cleistopholis*  
35  
36 310 *patens*, we believe minerals become concentrated in a similar way but without the  
37  
38 311 cylindrical process, merely by the adsorption by the decaying tree of mineral-  
39  
40 312 containing water, which evaporates upwards from the tree, leaving behind concen-  
41  
42 313 trated minerals, which are then accessed by chimpanzees chewing the decaying  
43  
44 314 wood.

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46 315 (b) In the case, of clay, we don't believe evaporation plays a part. The action of rain wa-  
47  
48 316 ter and/or river water on forest soil, especially in hollows under trees, leads to disso-  
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50 317 lution and/or dispersion of minerals from the clay material which contains a high  
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3 318 level of aluminium and surrounding soil which has a high iron content (Eggeling  
4 319 1947, Aufreiter 1997).  
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7 320 (c) In the case of termite mound soil, the actions of the termites themselves serve to concen-  
8  
9 321 trate the mineral elements in surrounding soil. The mechanisms by which this happens are  
10  
11 322 not clear and require further study. Studies by Sieber (1982) and Hesse (1955) focus on the  
12  
13 323 use of water by termites in processing surrounding soil before carrying it to the surface of  
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15 324 the mound. Turner (2005, 2011) describes, with associated videos, the process of drinking  
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17 325 and carrying soil by termites. In the case of forest termites, a further process may be im-  
18  
19 326 portant: the ingestion of organic matter in forest soil, thus having the incidental effect of in-  
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21 327 creasing the proportion of the mineral component. Further work is needed to elucidate the  
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23 328 causes of the differences between forest soil and termite mound soil.  
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### 330 **Summary and conclusions**

331 Termite mound soil provides the highest concentrations of aluminium and iron found in any  
332 of the dietary items at the sites studied here. The normal diet of chimpanzees, while high in  
333 calcium and moderately high in potassium and magnesium, lacks aluminium and copper and  
334 is low in other essential minerals. Sodium, low in the normal diet, is absent or in low con-  
335 centration in termite mound soil, which is thus not a dietary source of sodium for chimpan-  
336 zees. This absence is in stark contrast to the high concentration of sodium found in decaying  
337 wood, which is eaten (Fig 5, see also Reynolds et al. 2009). Thus, geophagy, meat eating,  
338 and insectivory all add to the intake of essential minerals obtained by chimpanzees. In both  
339 Budongo and Gombe, control forest soil taken from just a few meters away from the ter-  
340 mite mounds contains substantially lower concentrations of potassium, aluminium and cop-  
341 per. Thus we can see a concentrating effect in termite mound soil for some minerals, with  
342 the notable exception of sodium. Termite mound soil at Mahale shows a similar pattern of

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3 343 minerals to those at Budongo and Gombe, with high levels of iron and aluminium, and mod-  
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5 344 erate levels of potassium and magnesium. We suggest three possible mechanisms by which  
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7 345 minerals become concentrated: evaporation of water in decaying wood, concentration after  
8  
9 346 transport by termites, and dissolution or dispersion of mineral elements in clay after leach-  
10  
11 347 ing of soil by water. Chimpanzees have discovered these sources of minerals and now ex-  
12  
13 348 ploit them sporadically as an adjunct to their normal diet of fruits, leaves and other plant  
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15 349 parts.  
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21 512 **Supporting information**

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24 513 **Video 1. Termite mound soil consumption.** Young adult male (Zig) in the Budongo Forest  
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26 514 Reserve, feeding on soil from a *Pseudacanthotermes spiniger* termite mound in 2011 (video  
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28 515 Anne-Marijke Schel, # 08-29-2011\_123144.  
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3 516 **Tables and Figures**  
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6 517 **Table 1. Termite species and sampling periods across sites.** TMS = termite mound soil, CTRL  
7 518 = control soil. VR = V Reynolds, APG = A Pascual-Garrido, KH = K Hosaka, MS = M Shimada.  
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Site	Date(s) collected	Samples (N)	Termite species	Collectors
Budongo	July 2015 – Oct 2017	39 TMS, 27 CTRL	<i>Pseudacanthotermes spiniger</i> and <i>Cubitermes ugandensis</i>	VR
Gombe	Dec 2015	12 TMS, 7 CTRL	<i>Macrotermes bellicosus</i> , <i>Macrotermes michaelsoni</i> and <i>Macrotermes subhyalinus</i>	APG
Mahale	Aug – Sept 2015	11 TMS, 0 CTRL	Likely <i>Pseudacanthotermes</i> spp.	KH MS

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523 **Table 2. Mineral element concentration in termite mound and control soil across sites.** All  
 524 mineral concentrations reported in mean mg/kg  $\pm$  standard deviations; Significant differ-  
 525 ences between termite mound and control soil are indicated in **bold**. Element key:  
 526 Al=aluminium, Ca=calcium, Cu=copper, Fe=iron, K=potassium, Mg=magnesium,  
 527 Mn=manganese, Na=sodium, P=phosphorus, S=sulphur, Zn=zinc

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Mineral element	Budongo			Gombe			Mahale
	TMS (n=39)	CTRL (n=27)	Kruskal-Wallis	TMS (n=12)	CTRL (n=7)	Kruskal-Wallis	TMS (n=11)
Na	5 $\pm 15$	14 $\pm 27$	$X^2 = 1.43$ ; $p = 0.232$	<b>0</b>	<b>47.1</b> $\pm 8$	$X^2 = 16.84$ ; $p < 0.0001$	41.9 $\pm 43$
K	<b>1080</b> $\pm 395$	<b>685</b> $\pm 90$	$X^2 = 25.5$ ; $p < 0.001$	1980 $\pm 724$	1197 $\pm 291$	$X^2 = 7.78$ ; $p = 0.005$	5140 $\pm 2659$
S	237 $\pm 171$	169 $\pm 188$	$X^2 = 2.94$ ; $p = 0.86$	<b>119</b> $\pm 50$	<b>339</b> $\pm 27$	$X^2 = 12.60$ ; $p < 0.0001$	279 $\pm 133$
P	<b>694 <math>\pm 219</math></b>	<b>524</b> $\pm 109$	$X^2 = 9.92$ ; $p = 0.002$	422 $\pm 115$	329 $\pm 35$	$X^2 = 2.86$ ; $p = 0.091$	264 $\pm 123$
Ca	3270 $\pm 3179$	2310 $\pm 1463$	$X^2 = 0.83$ ; $p = 0.361$	1030 $\pm 939$	466 $\pm 257$	$X^2 = 3.46$ ; $p = 0.063$	1720 $\pm 648$
Fe	49100 $\pm 19576$	43657 $\pm 15489$	$X^2 = 0.80$ ; $p = 0.372$	<b>44500</b> $\pm 6380$	<b>28200</b> $\pm 4728$	$X^2 = 12.00$ ; $p = 0.001$	32100 $\pm 3235$
Zn	4.06 $\pm 15$	0	$X^2 = 3.34$ ; $p = 0.068$	0	0	N/A	455 $\pm 293$
Mn	1050 $\pm 421$	1130 $\pm 418$	$X^2 = 0.46$ ; $p = 0.498$	383 $\pm 244$	357 $\pm 119$	$X^2 = 0.00$ ; $p = 1.00$	585 $\pm 242$
Al	<b>18100</b> $\pm 4690$	<b>15300</b> $\pm 4182$	$X^2 = 5.36$ ; $p = 0.021$	<b>19400</b> $\pm 5428$	<b>11700</b> $\pm 2327$	$X^2 = 7.76$ ; $p = 0.005$	32600 $\pm 8016$
Cu	<b>20.86</b> $\pm 27$	<b>1.41</b> $\pm 4.5$	$X^2 = 12.62$ ; $p < 0.0001$	<b>92.3</b> $\pm 62$	<b>18.8</b> $\pm 29$	$X^2 = 7.39$ ; $p = 0.007$	10.2 $\pm 12$
Mg	670 $\pm 294$	604 $\pm 125$	$X^2 = 0.12$ ; $p = 0.912$	3520 $\pm 2996$	1600 $\pm 775$	$X^2 = 2.06$ ; $p = 0.151$	5210 $\pm 2751$

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539 **Table 3. Mean quantities of minerals in termite mound soil, decaying wood, clay, and**  
 540 **normal fruit + leaf diet (mg/kg) in Budongo samples.** All mineral concentrations reported in  
 541 mean mg/kg  $\pm$  standard deviations; Significant differences between termite mound and  
 542 other sources are indicated in **bold**. Element key: Al=aluminium, Ca=calcium, Cu=copper,  
 543 Fe=iron, K=potassium, Mg=magnesium, Mn=manganese, Na=sodium, P=phosphorus. <sup>1</sup>Data  
 544 taken from Reynolds et al., 2015; <sup>2</sup>Data taken from Reynolds et al., 2012.

Mineral element	Termite mound soil (n=39)	Clay soil <sup>1</sup> (n=10)	Decaying wood <sup>1,2</sup> (n=31)	Normal diet <sup>2</sup> (n=24)	Kruskal-Wallis
<b>Na</b>	<b>5</b> $\pm 15$	<b>234</b> $\pm 228$	<b>3032</b> $\pm 3826$	<b>293</b> $\pm 507$	$X^2 = 84.33; p < 0.0001$
<b>K</b>	<b>1080</b> $\pm 395$	<b>2528</b> $\pm 3613$	<b>9478</b> $\pm 14282$	<b>4074</b> $\pm 6485$	$X^2 = 37.13; p < 0.0001$
<b>P</b>	<b>694</b> $\pm 219$	<b>414</b> $\pm 534$	<b>1049</b> $\pm 2107$	<b>851</b> $\pm 964$	$X^2 = 9.36; p < 0.025$
<b>Ca</b>	<b>3270</b> $\pm 3179$	<b>2381</b> $\pm 3003$	<b>4221</b> $\pm 5675$	<b>13315</b> $\pm 30648$	$X^2 = 17.75; p < 0.0001$
<b>Fe</b>	<b>49100</b> $\pm 19576$	<b>8720</b> $\pm 3080$	<b>141</b> $\pm 152$	<b>649</b> $\pm 1310$	$X^2 = 82.04; p < 0.0001$
<b>Mn</b>	<b>1050</b> $\pm 421$	<b>306</b> $\pm 252$	<b>183</b> $\pm 369$	<b>66</b> $\pm 69$	$X^2 = 67.67; p < 0.0001$
<b>Al</b>	<b>18100</b> $\pm 4690$	<b>7885</b> $\pm 5245$	<b>0</b>	<b>0</b>	$X^2 = 94.83; p < 0.0001$
<b>Cu</b>	<b>20.9</b> $\pm 27$	<b>17</b> $\pm 13$	<b>0</b>	<b>0</b>	$X^2 = 40.36; p < 0.0001$
<b>Mg</b>	<b>670</b> $\pm 294$	<b>1012</b> $\pm 1165$	<b>2240</b> $\pm 2071$	<b>1557</b> $\pm 1272$	$X^2 = 18.71; p < 0.0001$

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3 552 **Figure 1. Termite mound (*Pseudacanthotermes spiniger*) in the Budongo Forest, Uganda.**  
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**Figure 2. Site where chimpanzee has removed a piece of termite mound soil, Budongo Forest, Uganda.**

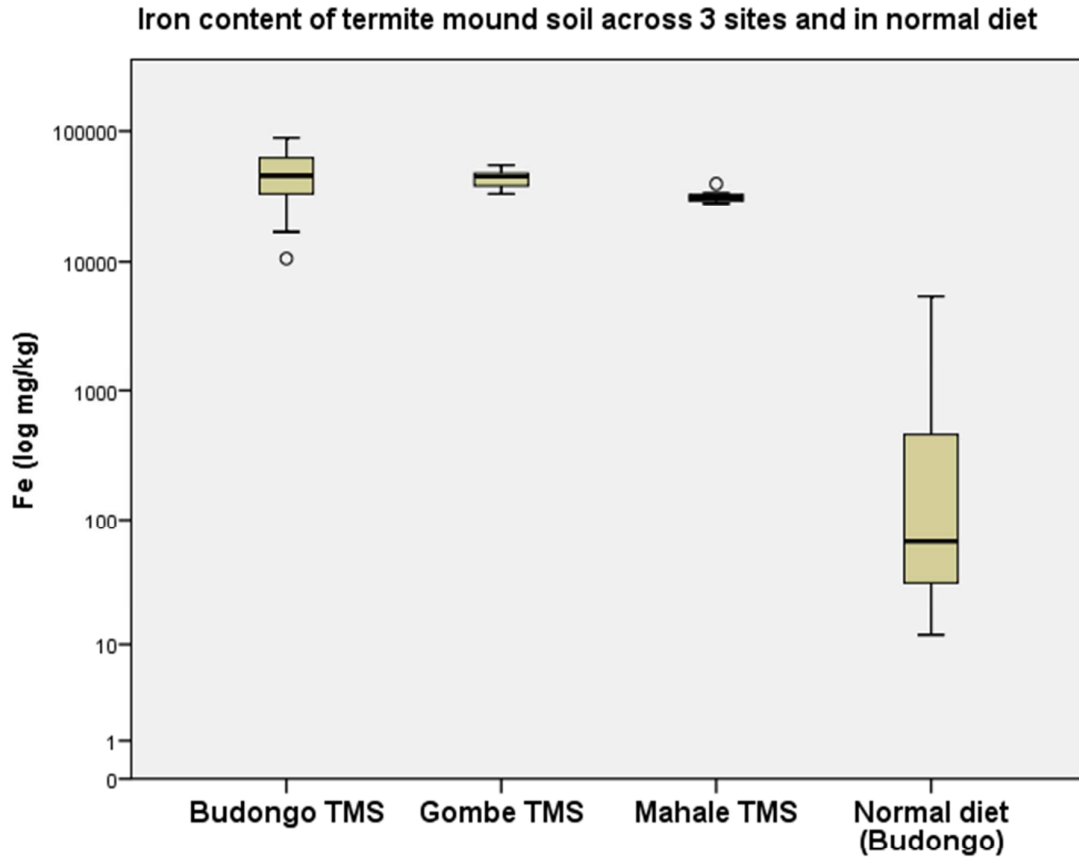


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563 Fig. 3 Iron content of termite mound soil at Budongo, Gombe, Mahale and in the normal diet of  
564 chimpanzees at Budongo



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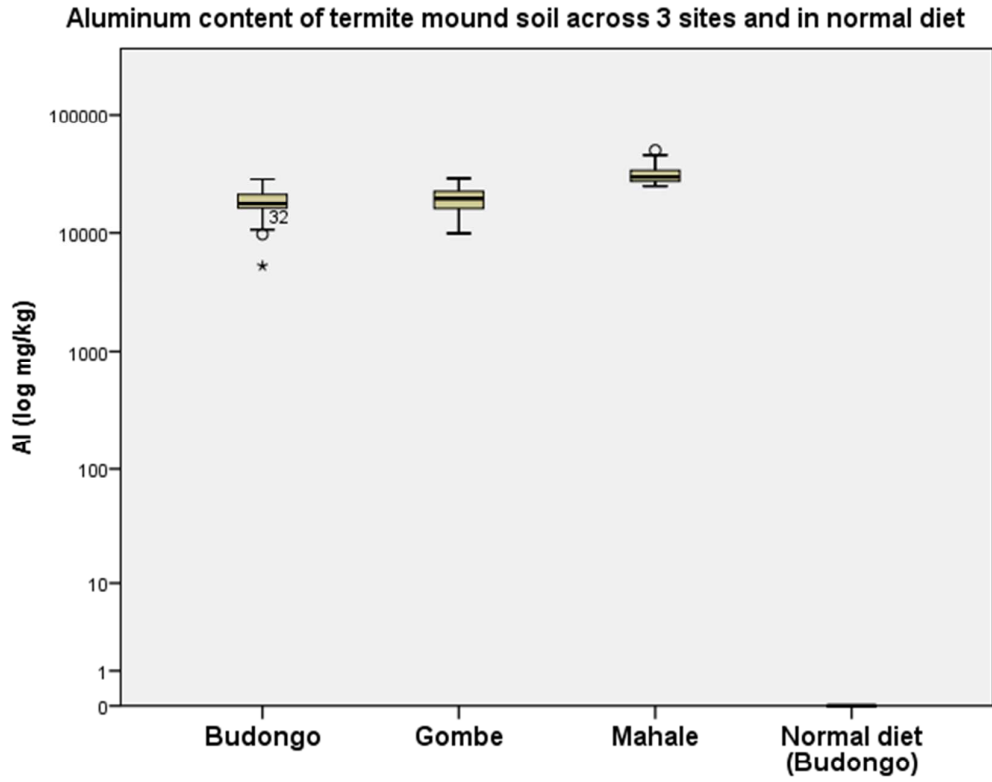
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575 Fig. 4 Aluminium content of termite mound soil at Budongo, Gombe, Mahale and in the normal diet  
576 of chimpanzees at Budongo

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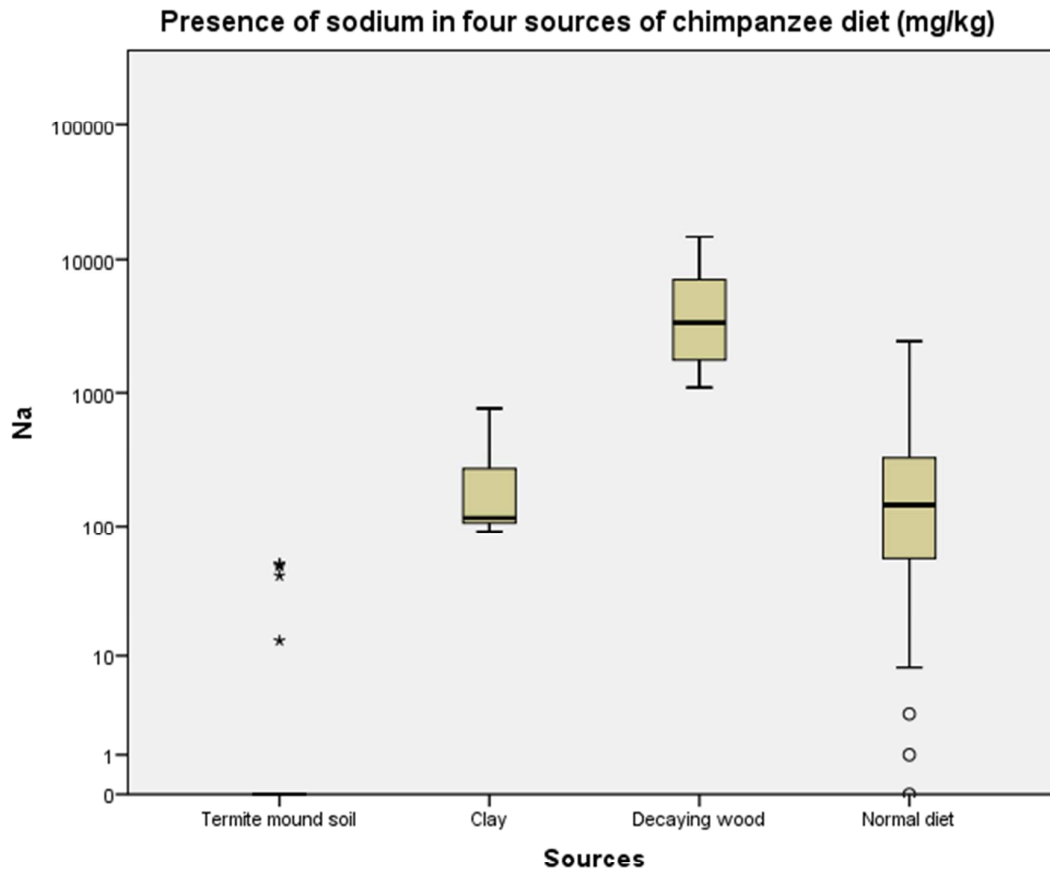
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591 Fig. 5 Presence of sodium in four sources of chimpanzee diet – Budongo data



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- Termite mound soil provides the highest concentrations of aluminium and iron found in any of the dietary items at the sites studied hitherto.
- We describe concentrating mechanisms in termite mound soil for some minerals.
- Chimpanzees have discovered these sources of minerals and how to exploit them.