

1 **Possible mineral contributions to the diet and health of wild chimpanzees in**
2 **three East African forests.**

3

4 Running title: Mineral contributions to chimpanzee diet

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15

16 **Abstract**

17 We present new data on the ingestion of minerals from termite mound soil by East African
18 chimpanzees (*Pan troglodytes schweinfurthii*) living in the Budongo Forest Reserve, Uganda,
19 and the Gombe National Park and the Mahale Mountains National Park, Tanzania. Termite
20 mound soil is here shown to be a rich source of minerals, containing high concentrations of
21 iron and aluminium. Termite mound soil is not, however, a source of sodium. The concen-
22 trations of iron and aluminium are the highest yet found in any of the mineral sources con-
23 sumed. Levels of manganese and copper, though not so high as for iron and aluminium, are
24 also higher than in other dietary sources. We focus on the contribution of termite mound
25 soil to other known sources of mineral elements consumed by these apes, and compare the
26 mineral content of termite soil with that of control forest soil, decaying wood, clay, and the
27 normal plant-based chimpanzee diet at Budongo. Samples obtained from Mahale Moun-
28 tains National Park and Gombe National Park, both in Tanzania, show similar mineral distri-
29 bution across sources. We suggest three distinct but related mechanisms by which minerals
30 may come to be concentrated in the above-mentioned sources, serving as potentially im-
31 portant sources of essential minerals in the chimpanzee diet.

32

33 **Keywords:** geophagy; *Pan troglodytes*; termite mound soil, minerals; diet; chimpanzees;
34 Uganda; Tanzania

35 **Introduction**

36 Some bird and mammalian species, including elephants, macaques, tamarins, gorillas, chim-
37 panzees and humans (Wilson 2003), consume soil of a variety of kinds, often in the form of
38 clay. Geophagy is widespread and has been observed on all continents inhabited by humans
39 and nonhuman primates (Pebsworth et al. 2018), with archaeological evidence suggesting
40 its practice to be as old as 2 million years (Clark, 2001). Though the most prominent causes
41 of geophagy remain unclear (Pebsworth et al., 2018), the practice of geophagy increases
42 micronutrient intake, which may have nutritional value, and other benefits such as the de-
43 toxification of harmful compounds such as alkaloids in the diet (Klaus, Klaus-Hugi and
44 Schmid, 1998), protection against infection by parasites and pathogens (Knezevich 1998),
45 and alleviation of gastro-intestinal upsets (Mahaney et al., 1996; Young 2010). As pointed
46 out by Pebsworth and colleagues (2018), in a review of the literature in this field, the total
47 elemental composition of soil may not reflect the amount of minerals available for the con-
48 sumer, and *in vitro* studies are needed to determine bioavailability of mineral elements eat-
49 en in the course of geophagy (Pebsworth et al., 2013; Seim et al., 2013; Wilson 2003). Prob-
50 ably no single characteristic of soils eaten by animals, including humans, can account for
51 their consumption (Abrahams, 1999; Wilson, 2003; Young et al., 2011), with mineral sup-
52 plementation, medical, and detoxification functions all playing a part (Aufreiter, Hancock,
53 Mahaney, Strambolic-Robb and Sanmagudas, 1997; Aufreiter et al., 2001; Ketch, Malloch,
54 Mahaney and Huffman, 2001; Mahaney, 1993; Mahaney et al., 1999; Pebsworth et al.,
55 2018; Vermeer and Ferrell, 1985; Wilson, 2003; Young 2010). Furthermore, geophagy may
56 not always be beneficial as soil may contain soil-transmitted helminths, heavy metals and
57 increase the risk of predation (Link et al., 2011; Matsubayashi et al., 2007., Pebsworth et al.,
58 2012).

59

60 The typical diet of wild chimpanzees in the Budongo Forest, Uganda, is typical of East Afri-
61 can chimpanzee groups, and consists primarily of fruits and leaves, with additional flowers,
62 bark, and pith (Reynolds 2005). Besides these plant-based items, meat and insects are eaten
63 sporadically when they become available. Both meat, obtained primarily by killing monkeys
64 (Nishida, Uehara and Nyundo, 1979; Goodall, 1986; Mitani and Watts, 2001; Newton-Fisher,
65 Notman and Reynolds, 2002) and insects, for example termites (O'Malley and Power 2014),
66 are highly nutritious sources of minerals as well as proteins, fats and other dietary require-
67 ments. However, the bulk of the food eaten by wild chimpanzees is plant-based and this
68 constitutes 80% or more of the daily diet of most individuals. While high in some minerals
69 e.g. potassium and calcium, the Budongo chimpanzees' diet lacks (or has low quantities) of
70 others e.g. copper, manganese, and sodium, and, as a result, they need to locate these min-
71 erals from other sources (Reynolds, Lloyd, Babweteera and English, 2009). Earlier work
72 (Reynolds et al., 2009; Reynolds, Lloyd and English, 2012; Reynolds et al., 2015) explored a
73 number of dietary supplements for mineral acquisition, namely decaying pith of *Raphia fa-*
74 *rinifera* and the decaying wood of *Cleistopholis patens*, which provide appreciable amounts
75 of sodium (Reynolds et al., 2009, 2012), and clay, which provides substantial amounts of
76 iron (Reynolds et al., 2015). In this paper we show that termite mound soil is a further valu-
77 able source of minerals eaten by chimpanzees in the Budongo Forest Reserve, Uganda, by
78 the Kasekela group at Gombe National Park and by the M group at the Mahale Mountains
79 National Park (Aufreiter et al., 2001).

80

81 Some discussion revolves around the extent of bioavailability of the iron ingested in soils,
82 including termite mound soil (Aufreiter et al., 2001; Seim et al., 2013). In part this resolves

83 itself into the question of whether the iron is in ferric (Fe^{3+}) or ferrous (Fe^{2+}) form. If the
84 former, it is not bioavailable; if the latter it is. Experimental work (Aufreiter et al., 2001) us-
85 ing a medium with low pH to simulate digestive conditions suggests that most of the iron in
86 soil is in ferric form and only a small part is ferrous. This finding suggests that the nutritional
87 value of ingested termite mound soil may be limited. However we should note that in hu-
88 mans a ferric reductase enzyme, duodenal cytochrome B, reduces ferric Fe^{3+} to Fe^{2+} (McKie
89 et al., 2001). This enzyme, if present in chimpanzees, as seems likely, serves to increase the
90 bioavailability of iron ingested in termite mound soil. If present, ferrihydrite, a hydrous ferric
91 oxide mineral, is likely to be solubilised (Wilson, 2003). Mahaney et al (1997) concluded that
92 in geophagy soils eaten by chimpanzees in the Kibale Forest, Uganda, 20% of ingested iron
93 was bioavailable, sufficient for nutritional significance. In a study of soils eaten by humans
94 and sold in local markets in Uganda, it was concluded that consumption of 5g of soil con-
95 tributed 19-25% of daily needs for iron (Abrahams and Parsons, 1997; Abrahams 1997);
96 however, more recent work suggests that some iron in soil may not be bioavailable, and
97 that some soil types may inhibit iron absorption from food (Seim et al., 2013). Geissler et al.
98 (1998), by contrast, found that despite consuming 30g daily of iron-rich termite mound soil,
99 anaemia remained prevalent in a human population in Kenya. Pregnant women were par-
100 ticularly prone to eating clays in Uganda and other tropical countries, although consumption
101 occurs in non-pregnant women and men (Huebl et al., 2016). In western Kenya, approxi-
102 mately half of pregnant women preferred termite soil (van Huis 2017). In northern Uganda a
103 greater diversity of soil types were eaten during gestation, and only pregnant women regu-
104 larly ate termite soil (Huebl et al., 2016). Pregnant Chacma baboons (*Papio ursinus*) spent
105 more time consuming iron-rich clay at monitored geophagy sites in Western Cape, South
106 Africa than baboons of other age-sex classes (Pebsworth, Bardi and Huffman, 2011).

107

108 Whereas the majority of minerals discussed in this paper can be regarded as either major
109 minerals essential for life or minor minerals required only as trace elements, aluminium is
110 neither of these and is not essential for life. Its ingestion in termite mound soil, probably in
111 the form of kaolinite (Johns and Duquette, 1991; Mahaney et al., 1995) and in some cases
112 gibbsite (Bolton, Campbell and Burton, 1998), probably serves medicinal functions, by re-
113 ducing acidity in the gut and neutralising plant toxins such as condensed tannins (Hladik,
114 1977; Goodall, 1986). Condensed tannins are ingested by chimpanzees on a daily basis at
115 Budongo, being found at high concentrations in several species of figs (*Ficus sp*), particularly
116 in the seed component. One fig species with a high concentration of condensed tannins, *Fi-*
117 *cus sur*, is the second most frequently eaten food of the Budongo chimpanzees. Condensed
118 tannins thus appear to be well tolerated by chimpanzees (Reynolds, Plumtre, Greenham and
119 Harbone, 1998; Wrangham, 1993; Aufreiter et al., 2001).

120

121 Termite mound soil eating is directed to specific species of termites (Uehara, 1982) and ap-
122 pears to be an opportunist, brief, and largely individual activity, occurring when the animals
123 pass by a termite mound in the forest, often moving from one vegetative feeding site to an-
124 other (Nishida & Uehara 1983; Goodall, 1986). Observations by researchers and field assis-
125 tants indicate that “Gombe chimpanzees eat termite mound soil, on average, once a day”
126 (Wrangham, 1977) and the same may be true at Mahale and Budongo. Anecdotal reports
127 suggest that at all three sites termite mound soil eating is more frequent among females
128 than males, but quantitative data are lacking. Termite mounds present a hard surface (Fig-
129 ure 1) and chimpanzees either bite off a piece with their teeth or break off a piece with their
130 fingers (Figure 2). At Mahale, chimpanzees eat the soil of termite mounds frequently

131 through the year. While consumption can be sometimes linked to times of gastrointestinal
132 distress (Mahaney et al. 1996), it may also allow chimpanzees to assess additional feeding
133 opportunities. The K-group of chimpanzees at Mahale were reported, before their disap-
134 pearance, to vary the technique they use to feed on termites with the colony's reproductive
135 cycle. In addition to direct nutritional benefits, feeding on termite soil may provide addi-
136 tional cues that allow selection of the most effective technique for subsequent consumption
137 of the termites themselves (Uehara, 1982). At Gombe, about once a day, as they pass ter-
138 mite mounds, chimpanzees pick off and eat a "walnut" sized piece of termite mound soil
139 (Goodall, 1986; Mahaney, Hancock, Aufreiter and Huffman, 1996; Huffman, 1997). Time
140 spent feeding on termite mound soil is short: at Mahale, 32 bouts of geophagy were meas-
141 ured and the mean duration was 1.7 min, range 1-8 min (Uehara, 1982). Co-feeding in large
142 groups on termite mound soil, seen for example when feeding on other soils such as clay,
143 has not been observed. And, unlike clay, termite mound soil is not eaten with leaves. At Bu-
144 dongo, if termites are present in termite mound soil, they are also eaten (Newton-Fisher,
145 1999), but use of tools for termite fishing has not been observed at Budongo, possibly be-
146 cause termite mounds of *Pseudacanthotermes* are less fishable, having few or no external
147 holes (Collins & McGrew, 1985), unlike those of *Macrotermes* species. At Mahale, use of
148 tools for termite fishing by the M group has only been seen occasionally (Takahata, 1982);
149 while at Gombe, chimpanzees termite fish year around, though concentrate this activity
150 around the wet months (Goodall, 1986; Uehara, 1982). Goodall (1986:256) also refers to
151 Wrangham's 1977 study at Gombe: "Analysis of samples of termite clay ... revealed substan-
152 tial quantities of potassium, magnesium and calcium and traces of copper, manganese, zinc,
153 and sodium ... feeding on termite clay may be to neutralise tannins and other poisons pre-
154 sent in plant foods (Hladik, 1977)". Soil recovered from a termite mound eaten by chimpan-

155 zeas at Mahale contained a relatively high concentration of aluminium (10%), iron (3%) and
156 sodium (0.5%). Metahalloysite was the dominant mineral found, which authors attribute a
157 possible role as a pharmaceutical agent to alleviate intestinal upset (Mahaney et al. 1996).

158

159 In this paper we explore the concentrations of mineral elements in termite mound soil
160 across three sites where chimpanzee have been well studied for decades: Gombe and Ma-
161 hale, Tanzania (Goodall, 1968; Nishida, 1968) and Budongo, Uganda (Reynolds, 2005), as
162 compared to control soil samples and other dietary sources. We go on to provide possible
163 explanations for the mechanisms by which mineral elements are concentrated in different
164 soil and plant-based sources.

165

166

167 **Methods**

168 **Subjects and sites**

169 Data were collected in the Budongo Forest Reserve, in north-western Uganda; and the
170 Gombe National Park and the Mahale Mountains National Park, both in western Tanzania.
171 Subjects at each of the three sites sampled were all well identified wild East African chim-
172 panzees (*Pan troglodytes schweinfurthii*), whose communities have been habituated to ob-
173 servation for several decades, (*Budongo*, 28-years, Hobaiter et al., 2017; Newton-Fisher,
174 1999; Reynolds, 2005; Reynolds et al., 2015. *Gombe*, 58-years, Goodall, 1968, 1986; Wrang-
175 ham, 1977. *Mahale M-group*, 51-years, Mahaney et al., 1999; Nakamura & Nishida, 2012;
176 Nishida, 1968; Nishida et al., 1979, 1983; Uehara, 1982). Males and females of all age
177 groups, except infants (aged 0-5 years old) were seen eating at the termite mounds from
178 which samples were collected. Unfortunately consumption of soil was not reliably recorded

179 with the long-term behavioural observations, so we are unable to provide frequency or
180 rates of soil consumption behaviour. Samples described here were collected between July
181 2015 and October 2017. Termite species are shown in Table 1.

182

183 **Soil sample collection**

184 Across sites, termite mound soil samples were collected by removing a 10-15g piece of
185 mound soil from a termite mound, using a sterile knife. None of the collected samples con-
186 tained termites. Clean gloves were worn to prevent contamination from human sweat. In
187 addition, control samples were collected of forest soil. At Budongo, control samples were
188 taken from forest soil 1-3m laterally from the termite mound and 15-20cm deep. At Gombe
189 control samples were taken from forest soil 1m laterally from the termite mound and 15-
190 20cm deep. Control samples were not collected at Mahale. All samples were put into indi-
191 vidual new plastic bags, marked with date, collector, block number (an indication of location
192 within the chimpanzee territory), and sample number, and taken back to base camp where
193 they were dried at a temperature of 40° C until fully dry. Five grams of each dried sample
194 was then transferred to new sterile plastic container tubes for onward shipment to the UK
195 under license.

196

197 **Laboratory Analysis of Soil Samples**

198 The soil samples were dried to constant weight in an oven at 105°C for 6 hours. The total
199 mass of the dried material was determined. Duplicate samples were prepared by taking 0.1g
200 of the material and 3ml of Aqua Regia in a 10ml centrifuge tube. The samples were digested
201 in a water bath at 85°C for 3 hours. 7ml of ultrapure Type 1 water was then added to each
202 sample and the samples mixed using a vortex mixer. A 1ml aliquot of each sample was dilut-

203 ed 10 fold with Type 1 water for analysis. The elemental content of each sample was then
204 determined using a Perkin Elmer Optima 2100 DV Inductively Coupled Plasma Optical Emis-
205 sion Spectrometer (ICP-OES). Standards and a blank were made up at 2, 4, 6, 8 and 10 ppm
206 concentrations with 3% HNO₃ and three replicates of each element were measured. Each
207 sample was analysed in triplicate and the average of the triplicate analysis taken for each
208 duplicate. The mean of the duplicate analyses of the individual soil samples was then taken
209 to be representative of that soil sample. The elemental content per kg of dried material was
210 calculated from the raw data. In addition, we undertook preliminary X-ray Photoelectron
211 Spectroscopy (XPS) analysis of one paired control and termite soil sample using a Ther-
212 moFisher ESCALAB 250Xi X-ray Photoelectron Spectrometer to investigate any differences in
213 iron speciation. We include comparison data from two published studies that explored the
214 mineral content of decaying wood fed on by Sonso chimpanzees (Reynolds et al., 2015) and
215 the typical diet of Sonso chimpanzees (including fruits, leaves, and other plant parts; Reyn-
216 olds et al., 2012). However, we do not have accurate data available on the relative quantity
217 of these items consumed by the Sonso community; thus, we are unable to calculate the rel-
218 ative contribution specific food types, such as termite soil, make to total mineral consump-
219 tion.

220

221 **Statistical analyses**

222 The data for each variable were tested for normality of distributions and equality of error
223 variances. Where these assumptions were not upheld non-parametric tests were used. Re-
224 sults were considered significant at $\alpha=0.05$. All data were analysed using SPSS v24.

225

226

227 **Results**

228 Values are mg/kg except where otherwise stated. We found a wide variation in the concen-
229 tration of the mineral elements measured in termite mound and control soil samples (Table
230 2). Iron, aluminium, and potassium were the highest in both termite mound soil and control
231 samples across sites. Zinc, sodium and copper had the lowest concentrations in both soil
232 types (with the exception of Mahale where zinc was more abundant in termite mound soil,
233 see Table 2).

234

235 **Budongo**

236 Potassium, phosphorus, aluminium, and copper were all more concentrated in termite
237 mound soil than in control soil; no other minerals varied in their abundance between soil
238 types (Table 2). When compared with mineral concentration in the normal diet (data taken
239 from Reynolds et al., 2012, Table 3), potassium (Kruskal Wallis: $X^2= 0.95$ $p=0.329$) and phos-
240 phorus (Kruskal Wallis: $X^2= 0.80$ $p=0.373$) are found at similar concentrations in termite
241 mound soil. Concentrations of all other minerals measured differed. Termite mound soil had
242 concentrations of iron over 75 times higher (49.1 ± 19.6 g/kg, $n=39$) than found in the nor-
243 mal diet (649 ± 1309 mg/kg, $n=24$; Kruskal Wallis: $X^2= 44.1$ $p<0.001$); and a very large con-
244 centration of aluminium (termite mound soil $15,300 \pm 4690$ mg/kg, $n=39$), which is com-
245 pletely absent from the normal diet ($n=24$; Kruskal Wallis: $X^2= 46.4$ $p<0.001$). Of other min-
246 erals, calcium ($X^2= 9.09$ $p=0.003$), magnesium ($X^2= 5.13$ $p=0.024$) and sodium ($X^2= 44.1$
247 $p<0.001$) were higher in the normal diet, while manganese ($X^2= 43.9$ $p<0.001$) and copper
248 ($X^2= 18.6$ $p<0.001$) were higher in termite mound soil.

249

250 **Gombe**

251 As at Budongo, iron had the highest concentrations in both termite mound soil and control
252 samples from Gombe, followed by aluminium (see Table 2). Preliminary XPS analysis of the
253 speciation of iron showed no differences in the ratio of Fe³⁺ to Fe²⁺ between the termite
254 mound soil and the control samples, but provided strong indication of the removal of organ-
255 ic matter in the termite mound soil. Levels of magnesium were higher across Gombe soil
256 samples (n=19) than in Budongo soil samples (n=66; Mann-Whitney: U=71, p<0.001); with
257 concentrations in termite mound soil over 5 times higher in Gombe (Table 2; Mann-
258 Whitney: U=22, p<0.001). As at Budongo, zinc, sodium and copper had the lowest concen-
259 trations. Sodium was completely absent from termite mound soil at Gombe, but was pre-
260 sent in small amounts in control samples. So, as at Budongo, Gombe termite mound soil
261 provided high concentrations of iron and aluminium, together with some magnesium and
262 other minerals, with the notable exception of sodium. Concentrations of potassium, iron,
263 aluminium, and copper were all higher in termite mound than in control soil samples at
264 Gombe; concentrations of sodium and sulphur were lower (Table 2).

265

266 **Mahale**

267 As at Budongo and Gombe, iron and aluminium were present in the highest concentrations,
268 although at Mahale aluminium, rather than iron, was highest; at almost double the concen-
269 trations present in Budongo or Gombe (Table 2; Kruskal-Wallis: X²= 25.13; p<0.001). Also, as
270 at Budongo and Gombe, sodium and copper had the lowest concentrations at Mahale. None
271 of the three sites compared had a consistently higher or lower overall concentration of min-
272 erals in any particular soil type.

273

274 **Comparisons between termite mound soil, clay, decaying wood, and the normal diet of**
275 **fruit and leaves at Budongo**

276 We compare the mineral content in termite mound soil with that present in clay (data from
277 Reynolds et al 2015, Table 3), decaying wood (*Raphia farinifera* and *Cleistopholis patens*)
278 (data from Reynolds et al., Tables 1 and 2 combined), and the normal diet of fruit and leaves
279 at Budongo (data from Reynolds et al., 2012, Table 3). The differences between means
280 shown in Table 3 are significant for all minerals shown.

281

282

283 **Discussion**

284 Given the distance between the three sites (Budongo to Gombe 740km, Gombe to Mahale
285 180 km) there is a high degree of similarity in the concentration of soil minerals between
286 them. Termite mound soil represents a rich potential source of iron (Fig 3a) and aluminium
287 (Fig 3b), which are present in high concentrations at all three sites. Iron, if bioavailable, is an
288 essential dietary mineral, and aluminium may serve an important role in detoxification or
289 regulation of the gastro-intestinal system (Abrahams, 1997; Johns & Duquette, 1991; Ver-
290 meer & Ferrell, 1985). Other minerals are present and potentially available at lower concen-
291 trations, and there is absence or near absence of sodium in soils across all three sites. Thus,
292 a clear picture emerges of the potential contribution of termite mound soil to the mineral
293 intake of chimpanzees in East Africa and possibly elsewhere. While it has been suggested
294 that consumption of the soil may provide additional cues for subsequent consumption of
295 the termites (Uehara, 1982), we did not observe feeding on termites during this study and
296 termites were not present in the soil samples collected, and so we were unable to assess
297 this as a possible motivation for soil consumption.

298

299 The differences between termite mound soil and control samples observed in our data are
300 consistent with those found by Adams et al. (2017), Mahaney et al. (1996, 1999), Aufreiter
301 et al. (2001), and Sarcinelli et al. (2009). This widespread difference indicates a process
302 whereby some mineral elements become concentrated in soil of fungus-culturing termite
303 mounds (Mills et al. 2009; Seymour et al. 2014). What is the process? It could take place at
304 the stage of acquisition of soil by termites, which involves a prolonged process of embed-
305 ding grains of soil in ingested water and salivary secretions (Turner, 2005) after which they
306 are carried up into the mound to the building point. However, minerals that are relatively
307 scarce in control forest soil are also relatively scarce in termite mound soil. Sodium in par-
308 ticular, scarce in forest soil, is very low or absent (i.e. below measurement detection limits)
309 in termite mound soil (see also Tweheyo et al., 2006). The main process whereby minerals
310 become concentrated in termite mound soil is therefore unlikely to be selection by termites
311 and more likely, based on preliminary XPS data, to be due to the removal of organic matter.

312

313 Low values (or absence) of sodium in termite mound soil were found in the initial samples of
314 termite mound soil collected as part of a study of minerals in clay (n=5; Reynolds et al.,
315 2015). This finding is now validated by a larger sample size across three different sites. The
316 complete absence of sodium from termite mound soil at Gombe, while present in control
317 samples, could indicate avoidance or rejection of sodium by termites or that they consume
318 sodium for their own requirements. The latter may be the correct explanation. Kaspari et al.
319 (2009, 2014) showed experimentally that numbers of termites in the soil and litter decom-
320 position rates were higher in Amazonian forest plots to which sodium had been applied than
321 in control plots. Whether sodium consumption is a common attribute of termites or can ex-

322 plain the relative lack of sodium in Gombe termite mound soil is not known (Scheffrahn
323 pers. comm.).
324
325 High values of aluminium and iron and low values of sodium were also found by Mahaney et
326 al. (1996, 1997, 1999) and Tweheyo et al. (2006) who emphasised the possible medicinal
327 use of aluminium in clay in the form of metahalloysite. Metahalloysite has the same formula
328 as kaolinite, $\text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4$ (Brindley, Robinson and MacEwan, 1946) and is used by humans
329 (commercially in the form of Kaopectate) to treat gastro-intestinal complaints (Hunter,
330 1973; Mahaney et al., 1997, 1999; Johns and Duquette, 1991; Wilson, 2003; Fairhead, 2016).
331 Smectite and gibbsite are further possible contributors to the efficacy of termite mound soil
332 (Wilson, 2003). Higher concentrations of mineral elements in termite mound soil than in
333 surrounding control soil were found by Aufreiter et al. (2001) and Adams et al. (2017) in a
334 study of arboreal termitaria in Peru.

335

336 **Mineral accretion**

337 It is of great interest that chimpanzees appear to have discovered these three “hidden”
338 sources of minerals: plant-based, soil-based, and animal-generated. In two of the three
339 (plant-based and animal-generated) mineral concentration comes about as a result of water
340 evaporation. In each case, water containing minerals is drawn up in decaying wood by capil-
341 lary action, in the case of termite mounds transported by termites. In the third case, clay,
342 low levels of minerals occur in the forest substrate and these are leached out of the soil by
343 rain-water that collects in holes under trees.

344

345 At *Raphia farinifera* and *Cleistopholis patens* sites, chimpanzees chew the fibrous, decaying
346 wood containing minerals left behind after evaporation, following which they spit out
347 ‘wedges’ of fibrous matter. At clay sites it appears that the minerals are ingested by chim-
348 panzees by chewing the clay when it is in semi-solid form, or extracting it from clay-water
349 with the use of leaf or moss sponges (Reynolds et al., 2015). At termite mound soil sites,
350 chimpanzees chew pieces of mound soil in a similar way to the way they chew clay.
351 In each of the above cases, a low level of minerals exists in the environment, too dispersed
352 and at concentrations too low for detection and acquisition by large mammals such as
353 chimpanzees. Concentration of minerals may come about in three ways:

354 (a) In the case of decaying *Raphia farinifera* palms, and *Cleistopholis patens* trees, these
355 are located in swamp forest which periodically floods, bringing in river water which
356 contains low levels of mineral elements leached from the soil and rocks along its
357 course. These elements are in low concentration (Reynolds et al., 2009, 2012, 2015).
358 We suggest that the decaying roots and pith of *Raphia* use capillary action to draw
359 swamp water upwards inside the tree’s vertical, fibrous, pith-filled trunk. Because
360 the head of the *Raphia* palm has previously fallen off after the tree fruited, the top of
361 the trunk is now open and the whole trunk forms a cylinder filled with fibrous pith.
362 Water containing low levels of minerals can enter this cylinder from below and rises
363 up the fibres. As water evaporates from the top of the cylinder, it will leave its min-
364 eral content behind. As a result we speculate that this becomes concentrated, and it
365 is this source that the chimpanzees have learned to access by making a hole in the
366 bark of the lower trunk (see Reynolds et al., 2009). In the case of *Cleistopholis pat-*
367 *ens*, we believe minerals become concentrated in a similar way but without the cy-
368 lindrical process, merely by the adsorption by the decaying tree of mineral-

369 containing water, which evaporates upwards from the tree, leaving behind concen-
370 trated minerals, which are then accessed by chimpanzees chewing the decaying
371 wood.

372 (b) In the case, of clay, we don't believe evaporation plays a part. The action of rain wa-
373 ter and/or river water on forest soil, especially in hollows under trees, leads to disso-
374 lution and/or dispersion of minerals from the clay material which contains a high
375 level of aluminium and surrounding soil which has a high iron content (Eggeling
376 1947, Aufreiter 1997).

377 (c) In the case of termite mound soil, the actions of the termites themselves serve to
378 concentrate the mineral elements in surrounding soil. The mechanisms by which this
379 happens are not clear and require further study. Studies by Sieber (1982) and Hesse
380 (1955) focus on the use of water by termites in processing surrounding soil before
381 carrying it to the surface of the mound. Turner (2005, 2011) describes, with associat-
382 ed videos, the process of drinking and carrying soil by termites. In the case of forest
383 termites, a further process may be important: the ingestion of organic matter in for-
384 est soil, thus having the incidental effect of increasing the proportion of the mineral
385 component and potentially making the termite mound soil more palatable following
386 the removal of unpalatable organic components. Further work is needed to elucidate
387 the causes of the differences between forest soil and termite mound soil.

388

389 **Summary and conclusions**

390 Termite mound soil provides the highest concentrations of aluminium and iron
391 found in any of the dietary items at the sites studied here. The normal diet of chim-

392 panzees, while high in calcium and moderately high in potassium and magnesium,
393 lacks aluminium and copper and is low in other minerals. Sodium, low in the normal
394 diet, is absent or in low concentration in termite mound soil, which is thus not a die-
395 tary source of sodium for chimpanzees. This absence is in stark contrast to the high
396 concentration of sodium found in decaying wood, which is eaten (Fig 3c, see also
397 Reynolds et al. 2009). Thus, geophagy, meat eating, and insectivory (O'Malley and
398 Power, 2014) all add potential sources of important minerals for chimpanzees. In
399 both Budongo and Gombe, control forest soil taken from just a few meters away
400 from the termite mounds contains substantially lower concentrations of potassium,
401 aluminium and copper. Thus we can see a concentrating effect in termite mound soil
402 for some minerals, with the notable exception of sodium. Termite mound soil at Ma-
403 hale shows a similar pattern of minerals to those at Budongo and Gombe, with high
404 levels of iron and aluminium, and moderate levels of potassium and magnesium. We
405 suggest three possible mechanisms by which minerals become concentrated: evapo-
406 ration of water in decaying wood, concentration after transport by termites, and dis-
407 solution or dispersion of mineral elements in clay after leaching of soil by water.
408 Chimpanzees have discovered these potentially rich sources of minerals. If bioavaila-
409 ble, they would represent important additional opportunities to supplement the in-
410 take of nutritive-minerals available in their normal diet of fruits, leaves and other
411 plant parts, or (in the case of aluminium) otherwise regulate the functioning of the
412 gastro-intestinal system.

413

414

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611

612 **Acknowledgments**

613 We thank Jessica Rothman and an anonymous reviewer for their helpful comments that

614 substantially improved our manuscript. At the Budongo Conservation Field Station we are

615 indebted to Aliyo Jacob and Chandiya Bosco, Geresomu Muhumuza, Monday Gideon, Geof-

616 frey Muhanguzi, Caroline Asimwe, and P. Nyeko for termite identification. For research

617 permission and export permits in Uganda we are grateful to the Uganda National Council for

618 Science and Technology, the National Forest Authority, and the Uganda Wildlife Authority.

619 For securing the necessary permission to import samples to UK for analysis we are grateful

620 to Raymond Ward of the University of Brighton. For undertaking the preliminary XPS analy-

621 sis at short notice we are indebted to Dr Santanu Ray of the Surface Analysis Laboratory at

622 the University of Brighton. For help at Gombe National Park we are indebted to Anthony

623 Collins, Deus Mjungu, Nuhu Japhary Buke, Matendo Msafiri Katoto, and to Rudolf
624 Scheffrahn, University of Florida, USA, for termite identification. At Mahale Mountains Na-
625 tional Park we are grateful to Michio Nakamura, Kazuhiko Hosaka and Masaki Shimada. For
626 research permission in Gombe National Park and Mahale Mountains National Park we are
627 indebted to the Tanzania National Parks Service, the Tanzania Wildlife Research Institute,
628 and the Tanzania Commission for Science and Technology. For logistical assistance we
629 acknowledge The Jane Goodall Institute at Gombe and the Mahale Mountains Chimpanzee
630 Research Project at Mahale. We thank Anne-Marijke Schel for permission to use the video
631 material in Supporting Information, and J.P.E.C. Darlington, Derek Pomeroy, S. Sutherland,
632 and Andrew Smith for their comments and advice. For financial support we acknowledge
633 the Mohamed bin Zayed Species Conservation Fund, the Royal Zoological Society of Scot-
634 land, the Leverhulme Trust, and the Boise Fund.

635

636 **Supporting information**

637 **Video 1. Termite mound soil consumption.** Young adult male (Zig) in the Budongo Forest
638 Reserve, feeding on soil from a *Pseudacanthotermes spiniger* termite mound in 2011 (video
639 Anne-Marijke Schel, # 08-29-2011_123144).

640 **Tables and Figures**

641 **Table 1. Termite species and sampling periods across sites.** TMS = termite mound soil, CTRL
 642 = 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>Macro-</i> <i>termes michaelsoni</i> and <i>Macro-</i> <i>termes subhyalinus</i>	APG
Mahale	Aug – Sept 2015	11 TMS, 0 CTRL	Likely <i>Pseudacanthotermes spp.</i>	KH MS

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647 **Table 2. Mineral element concentration in termite mound and control soil across sites.** All
 648 mineral concentrations reported in mean mg/kg \pm standard deviations; Significant differ-
 649 ences between termite mound and control soil are indicated in **bold**. We provide the NRC
 650 nutritional recommendations for comparison as % (where indicated) or mg.kg⁻¹ (National
 651 Research Council, 2003). Element key: Al=aluminium, Ca=calcium, Cu=copper, Fe=iron,
 652 K=potassium, Mg=magnesium, Mn=manganese, Na=sodium, P=phosphorus, S=sulphur,
 653 Zn=zinc

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Mineral element	Budongo			Gombe			Mahale	NRC
	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	$X^2= 1.43$; $p=0.232$	0	47.1 \pm 8	$X^2= 16.84$; $p<0.0001$	41.9 \pm 43	0.2%
K	1080 \pm 395	685 \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	0.4%
S	237 \pm 171	169 \pm 188	$X^2= 2.94$; $p=0.86$	119 \pm 50	339 \pm 27	$X^2= 12.60$; $p<0.0001$	279 \pm 133	-
P	694 \pm 219	524 \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	0.6%
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	0.8%
Fe	49100 \pm 19576	43657 \pm 15489	$X^2= 0.80$; $p=0.372$	44500 \pm 6380	28200 \pm 4728	$X^2= 12.00$; $p=0.001$	32100 \pm 3235	100
Zn	4.06 \pm 15	0	$X^2= 3.34$; $p=0.068$	0	0	N/A	455 \pm 293	20
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	20
Al	18100 \pm 4690	15300 \pm 4182	$X^2= 5.36$; $p=0.021$	19400 \pm 5428	11700 \pm 2327	$X^2= 7.76$; $p=0.005$	32600 \pm 8016	-
Cu	20.86 \pm 27	1.41 \pm 4.5	$X^2= 12.62$; $p<0.0001$	92.3 \pm 62	18.8 \pm 29	$X^2= 7.39$; $p=0.007$	10.2 \pm 12	20
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	0.08 %

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664 **Table 3. Mean quantities of minerals in termite mound soil, decaying wood, clay, and**
 665 **normal fruit + leaf diet (mg/kg) in Budongo samples.** All mineral concentrations reported in
 666 mean mg/kg ± standard deviations. Significant differences between termite mound and
 667 other sources are indicated in **bold**. We provide the NRC nutritional recommendation for
 668 comparison as % (where indicated) or mg.kg⁻¹ (National Research Council, 2003). Element
 669 key: Al=aluminium, Ca=calcium, Cu=copper, Fe=iron, K=potassium, Mg=magnesium,
 670 Mn=manganese, Na=sodium, P=phosphorus. ¹Data taken from Reynolds et al., 2015; ²Data
 671 on normal diet of Sonso chimpanzees includes fruits, leaves, and other plant parts; taken
 672 from Reynolds et al., 2012.

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Mineral element	Termite mound soil (n=39)	Clay soil ¹ (n=10)	Decaying wood ^{1,2} (n=31)	Normal diet ² (n=24)	NRC	Kruskal-Wallis
Na	5 ±15	234 ±228	3032 ±3826	293 ±507	0.2%	X²= 84.33; p<0.0001
K	1080 ±395	2528 ±3613	9478 ±14282	4074 ±6485	0.4%	X²= 37.13; p<0.0001
P	694 ±219	414 ±534	1049 ±2107	851 ±964	0.6%	X²= 9.36; p<0.025
Ca	3270 ±3179	2381 ±3003	4221 ±5675	13315 ±30648	0.8%	X²= 17.75; p<0.0001
Fe	49100 ±19576	8720 ±3080	141 ±152	649 ±1310	100	X²= 82.04; p<0.0001
Mn	1050 ±421	306 ±252	183 ±369	66 ±69	20	X²= 67.67; p<0.0001
Al	18100 ±4690	7885 ±5245	0	0	-	X²= 94.83; p<0.0001
Cu	20.9 ±27	17 ±13	0	0	20	X²= 40.36; p<0.0001
Mg	670 ±294	1012 ±1165	2240 ±2071	1557 ±1272	0.08 %	X²= 18.71; p<0.0001

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680 **Figure 1. Termite mound (*Pseudacanthotermes spiniger*) in the Budongo Forest, Uganda.**



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684 **Figure 2. Site where chimpanzee has removed a piece of termite mound soil, Budongo**
685 **Forest, Uganda.**



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