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

Running title: Mineral contributions to chimpanzee diet

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Abstract

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

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

Introduction

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

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

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

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

Termite mound soil eating is directed to specific species of termites (Uehara, 1982) and appears to be an opportunist, brief, and largely individual activity, occurring when the animals pass by a termite mound in the forest, often moving from one vegetative feeding site to another (Nishida & Uehara 1983; Goodall, 1986). Observations by researchers and field assistants indicate that “Gombe chimpanzees eat termite mound soil, on average, once a day” (Wrangham, 1977) and the same may be true at Mahale and Budongo. Anecdotal reports suggest that at all three sites termite mound soil eating is more frequent among females than males, but quantitative data are lacking. Termite mounds present a hard surface (Figure 1) and chimpanzees either bite off a piece with their teeth or break off a piece with their fingers (Figure 2). At Mahale, chimpanzees eat the soil of termite mounds frequently through the year. While consumption can be sometimes linked to times of gastrointestinal distress (Mahaney et al. 1996), it may also allow chimpanzees to assess additional feeding opportunities. The K-group of chimpanzees at Mahale were reported, before their disappearance, to vary the technique they use to feed on termites with the colony's reproductive cycle. In addition to direct nutritional benefits, feeding on termite soil may provide additional cues that allow selection of the most effective technique for subsequent consumption of the termites themselves (Uehara, 1982). At Gombe, about once a day, as they pass termite mounds, chimpanzees pick off and eat a "walnut" sized piece of termite mound soil (Goodall, 1986; Mahaney, Hancock, Aufreiter and Huffman, 1996; Huffman, 1997). Time spent feeding on termite mound soil is short: at Mahale, 32 bouts of geophagy were measured and the mean duration was 1.7 min, range 1-8 min (Uehara, 1982). Co-feeding in large groups on termite mound soil, seen for example when feeding on other soils such as clay, has not been observed. And, unlike clay, termite mound soil is not eaten with leaves. At Budongo, if termites are present in termite mound soil, they are also eaten (Newton-Fisher, 1999), but use of tools for termite fishing has not been observed at Budongo, possibly because termite mounds of *Pseudacanthotermes* are less fishable, having few or no external holes (Collins & McGrew, 1985), unlike those of *Macrotermes* species. At Mahale, use of tools for termite fishing by the M group has only been seen occasionally (Takahata, 1982); while at Gombe, chimpanzees termite fish year around, though concentrate this activity around the wet months (Goodall, 1986; Uehara, 1982). Goodall (1986:256) also refers to Wrangham's 1977 study at Gombe: "Analysis of samples of termite clay … revealed substantial quantities of potassium, magnesium and calcium and traces of copper, manganese, zinc, and sodium … feeding on termite clay may be to neutralise tannins and other poisons present in plant foods (Hladik, 1977)". Soil recovered from a termite mound eaten by chimpanzees at Mahale contained a relatively high concentration of aluminium (10%), iron (3%) and sodium (0.5%). Metahalloysite was the dominant mineral found, which authors attribute a possible role as a pharmaceutical agent to alleviate intestinal upset (Mahaney et al. 1996).

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

Methods

Subjects and sites

Data were collected in the Budongo Forest Reserve, in north-western Uganda; and the Gombe National Park and the Mahale Mountains National Park, both in western Tanzania. Subjects at each of the three sites sampled were all well identified wild East African chimpanzees (*Pan troglodytes schweinfurthii*), whose communities have been habituated to observation for several decades, (*Budongo*, 28-years, Hobaiter et al., 2017; Newton-Fisher, 1999; Reynolds, 2005; Reynolds et al., 2015. *Gombe*, 58-years, Goodall, 1968, 1986; Wrangham, 1977. *Mahale M-group*, 51-years, Mahaney et al., 1999; Nakamura & Nishida, 2012; Nishida, 1968; Nishida et al., 1979, 1983; Uehara, 1982). Males and females of all age groups, except infants (aged 0-5 years old) were seen eating at the termite mounds from which samples were collected. Unfortunately consumption of soil was not reliably recorded with the long-term behavioural observations, so we are unable to provide frequency or rates of soil consumption behaviour. Samples described here were collected between July 2015 and October 2017. Termite species are shown in Table 1.

Soil sample collection

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

Laboratory Analysis of Soil Samples

The soil samples were dried to constant weight in an oven at 105°C for 6 hours. The total mass of the dried material was determined. Duplicate samples were prepared by taking 0.1g of the material and 3ml of Aqua Regia in a 10ml centrifuge tube. The samples were digested in a water bath at 85°C for 3 hours. 7ml of ultrapure Type 1 water was then added to each sample and the samples mixed using a vortex mixer. A 1ml aliquot of each sample was diluted 10 fold with Type 1 water for analysis. The elemental content of each sample was then determined using a Perkin Elmer Optima 2100 DV Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES). Standards and a blank were made up at 2, 4, 6, 8 and 10 ppm concentrations with 3% HNO_3 and three replicates of each element were measured. Each sample was analysed in triplicate and the average of the triplicate analysis taken for each duplicate. The mean of the duplicate analyses of the individual soil samples was then taken to be representative of that soil sample. The elemental content per kg of dried material was calculated from the raw data. In addition, we undertook preliminary X-ray Photoelectron Spectroscopy (XPS) analysis of one paired control and termite soil sample using a ThermoFisher ESCALAB 250Xi X-ray Photoelectron Spectrometer to investigate any differences in iron speciation. We include comparison data from two published studies that explored the mineral content of decaying wood fed on by Sonso chimapnzees (Reynolds et al., 2015) and the typical diet of Sonso chimpanzees (including fruits, leaves, and other plant parts; Reynolds et al., 2012). However, we do not have accurate data available on the relative quantity of these items consumed by the Sonso community; thus, we are unable to calculate the relative contribution specific food types, such as termite soil, make to total mineral consumption.

Statistical analyses

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

Results

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

Budongo

Potassium, phosphorus, aluminium, and copper were all more concentrated in termite mound soil than in control soil; no other minerals varied in their abundance between soil types (Table 2). When compared with mineral concentration in the normal diet (data taken from Reynolds et al., 2012, Table 3), potassium (Kruskal Wallis: X^2= 0.95 p=0.329) and phosphorus (Kruskal Wallis: X^2= 0.80 p=0.373) are found at similar concentrations in termite mound soil. Concentrations of all other minerals measured differed. Termite mound soil had concentrations of iron over 75 times higher (49.1 ±19.6 g/kg, n=39) than found in the normal diet (649 ± 1309 mg/kg, n=24; Kruskal Wallis: X^2= 44.1 p<0.001); and a very large concentration of aluminium (termite mound soil 15,300 ±4690 mg/kg, n=39), which is completely absent from the normal diet (n=24; Kruskal Wallis: X^2= 46.4 p<0.001). Of other minerals, calcium (X^2= 9.09 p=0.003), magnesium (X^2= 5.13 p=0.024) and sodium (X^2= 44.1 p<0.001) were higher in the normal diet, while manganese (X^2= 43.9 p<0.001) and copper (X^2= 18.6 p<0.001) were higher in termite mound soil.

Gombe

As at Budongo, iron had the highest concentrations in both termite mound soil and control samples from Gombe, followed by aluminium (see Table 2). Preliminary XPS analysis of the speciation of iron showed no differences in the ratio of Fe^{3+} to Fe^{2+} between the termite mound soil and the control samples, but provided strong indication of the removal of organic matter in the termite mound soil. Levels of magnesium were higher across Gombe soil samples (n=19) than in Budongo soil samples (n=66; Mann-Whitney: U=71, p<0.001); with concentrations in termite mound soil over 5 times higher in Gombe (Table 2; Mann-Whitney: U=22, p<0.001). As at Budongo, zinc, sodium and copper had the lowest concentrations. Sodium was completely absent from termite mound soil at Gombe, but was present in small amounts in control samples. So, as at Budongo, Gombe termite mound soil provided high concentrations of iron and aluminium, together with some magnesium and other minerals, with the notable exception of sodium. Concentrations of potassium, iron, aluminium, and copper were all higher in termite mound than in control soil samples at Gombe; concentrations of sodium and sulphur were lower (Table 2).

Mahale

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

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

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

Discussion

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

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

Low values (or absence) of sodium in termite mound soil were found in the initial samples of termite mound soil collected as part of a study of minerals in clay (n=5; Reynolds et al., 2015). This finding is now validated by a larger sample size across three different sites. The complete absence of sodium from termite mound soil at Gombe, while present in control samples, could indicate avoidance or rejection of sodium by termites or that they consume sodium for their own requirements. The latter may be the correct explanation. Kaspari et al. (2009, 2014) showed experimentally that numbers of termites in the soil and litter decomposition rates were higher in Amazonian forest plots to which sodium had been applied than in control plots. Whether sodium consumption is a common attribute of termites or can explain the relative lack of sodium in Gombe termite mound soil is not known (Scheffrahn pers. comm.).

High values of aluminium and iron and low values of sodium were also found by Mahaney et al. (1996, 1997, 1999) and Tweheyo et al. (2006) who emphasised the possible medicinal use of aluminium in clay in the form of metahalloysite. Metahalloysite has the same formula as kaolinite, $Al_2Si_2O_5(OH)_4$ (Brindley, Robinson and MacEwan, 1946) and is used by humans (commercially in the form of Kaopectate) to treat gastro-intestinal complaints (Hunter, 1973; Mahaney et al., 1997, 1999; Johns and Duquette, 1991; Wilson, 2003; Fairhead, 2016). Smectite and gibbsite are further possible contributors to the efficacy of termite mound soil (Wilson, 2003). Higher concentrations of mineral elements in termite mound soil than in surrounding control soil were found by Aufreiter et al. (2001) and Adams et al. (2017) in a study of arboreal termitaria in Peru.

Mineral accretion

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

At *Raphia farinifera* and *Cleistopholis patens* sites, chimpanzees chew the fibrous, decaying wood containing minerals left behind after evaporation, following which they spit out 'wadges' of fibrous matter. At clay sites it appears that the minerals are ingested by chimpanzees by chewing the clay when it is in semi-solid form, or extracting it from clay-water with the use of leaf or moss sponges (Reynolds et al., 2015). At termite mound soil sites, chimpanzees chew pieces of mound soil in a similar way to the way they chew clay.

In each of the above cases, a low level of minerals exists in the environment, too dispersed and at concentrations too low for detection and acquisition by large mammals such as chimpanzees. Concentration of minerals may come about in three ways:

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

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

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

Summary and conclusions

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

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Acknowledgments

We thank Jessica Rothman and an anonymous reviewer for their helpful comments that substantially improved our manuscript. At the Budongo Conservation Field Station we are indebted to Aliyo Jacob and Chandiya Bosco, Geresomu Muhumuza, Monday Gideon, Geoffrey Muhanguzi, Caroline Asiimwe, and P. Nyeko for termite identification. For research permission and export permits in Uganda we are grateful to the Uganda National Council for Science and Technology, the National Forest Authority, and the Uganda Wildlife Authority. For securing the necessary permission to import samples to UK for analysis we are grateful to Raymond Ward of the University of Brighton. For undertaking the preliminary XPS analysis at short notice we are indebted to Dr Santanu Ray of the Surface Analysis Laboratory at the University of Brighton. For help at Gombe National Park we are indebted to Anthony

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

Supporting information

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

Tables and Figures

Table 1. Termite species and sampling periods across sites. TMS = termite mound soil, CTRL = control soil. VR = V Reynolds, APG = A Pascual-Garrido, KH = K Hosaka, MS = M Shimada.

Site	Date(s) collected	Samples (N)	Termite species	Collectors
Budongo	July 2015 – Oct 2017	39 TMS, 27 CTRL	*Pseudacanthotermes spiniger and Cubitermes ugandensis*	VR
Gombe	Dec 2015	12 TMS, 7 CTRL	*Macrotermes bellicosus, Macrotermes michaelseni and Macrotermes subhyalinus*	APG
Mahale	Aug – Sept 2015	11 TMS, 0 CTRL	Likely *Pseudacanthotermes spp.*	KH MS

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

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 ±15	14 ±27	X^2= 1.43; p=0.232	**0**	**47.1** ±8	**X^2= 16.84; p<0.0001**	41.9 ±43	**0.2%**
K	**1080 ±395**	**685 ±90**	**X^2= 25.5; p<0.001**	1980 ±724	1197 ±291	X^2= 7.78; p=0.005	5140 ±2659	**0.4%**
S	237 ±171	169 ±188	X^2= 2.94; p=0.86	**119** ±50	**339** ±27	**X^2= 12.60; p<0.0001**	279 ±133	-
P	**694 ±219**	**524 ±109**	**X^2= 9.92; p=0.002**	422 ±115	329 ±35	X^2= 2.86; p=0.091	264 ±123	0.6%
Ca	3270 ±3179	2310 ±1463	X^2= 0.83; p=0.361	1030 ±939	466 ±257	X^2=3.46; p=0.063	1720 ±648	**0.8%**
Fe	49100 ±19576	43657 ±15489	X^2= 0.80; p=0.372	**44500** ±6380	**28200** ±4728	**X^2= 12.00; p=0.001**	32100 ±3235	**100**
Zn	4.06 ±15	0	X^2= 3.34; p=0.068	0	0	N/A	455 ±293	**20**
Mn	1050 ±421	1130 ±418	X^2= 0.46; p=0.498	383 ±244	357 ±119	X^2= 0.00; p=1.00	585 ±242	**20**
Al	**18100 ±4690**	**15300 ±4182**	**X^2= 5.36; p=0.021**	**19400** ±5428	**11700** ±2327	**X^2= 7.76; p=0.005**	32600 ±8016	**-**
Cu	**20.86 ±27**	**1.41 ±4.5**	**X^2= 12.62; p<0.0001**	**92.3** ±62	**18.8** ±29	**X^2= 7.39; p=0.007**	10.2 ±12	20
Mg	670 ±294	604 ±125	X^2= 0.12; p=0.912	3520 ±2996	1600 ±775	X^2= 2.06; p=0.151	5210 ±2751	0.08 %

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

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%**	**X^2= 84.33; p<0.0001**
K	**1080** **±395**	**2528** **±3613**	**9478** **±14282**	**4074** **±6485**	**0.4%**	**X^2= 37.13; p<0.0001**
P	**694** **±219**	**414** **±534**	**1049** **±2107**	**851** **±964**	0.6%	**X^2= 9.36; p<0.025**
Ca	**3270** **±3179**	**2381** **±3003**	**4221** **±5675**	**13315** **±30648**	**0.8%**	**X^2= 17.75; p<0.0001**
Fe	**49100** **±19576**	**8720** **±3080**	**141** **±152**	**649** **±1310**	**100**	**X^2= 82.04; p<0.0001**
Mn	**1050** **±421**	**306** **±252**	**183** **±369**	**66** **±69**	**20**	**X^2= 67.67; p<0.0001**
Al	**18100** **±4690**	**7885** **±5245**	**0**	**0**	**-**	**X^2= 94.83; p<0.0001**
Cu	**20.9** **±27**	**17** **±13**	**0**	**0**	**20**	**X^2= 40.36; p<0.0001**
Mg	**670** **±294**	**1012** **±1165**	**2240** **±2071**	**1557** **±1272**	0.08 %	**X^2= 18.71; p<0.0001**

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

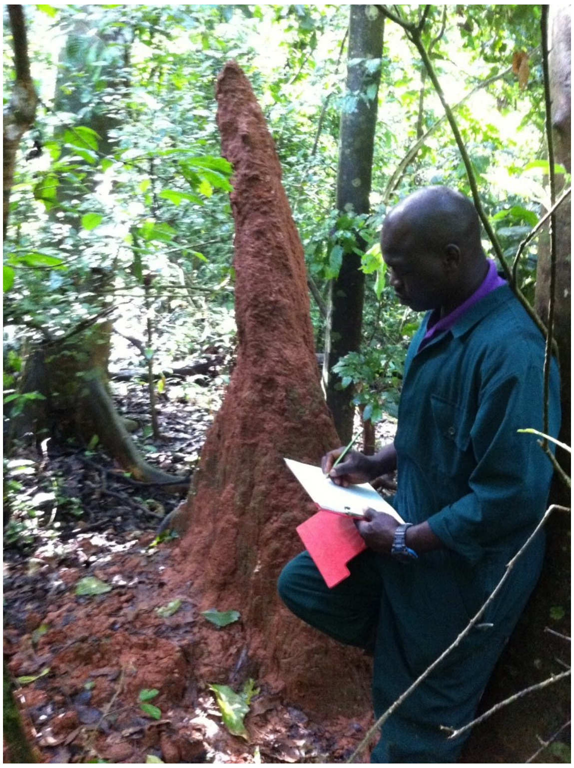

Figure 2. Site where chimpanzee has removed a piece of termite mound soil, Budongo Forest, Uganda.