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Spatial geochemistry influences the home range of elephants

Fiona Sach [a,b], Lisa Yon [c], Michelle D. Henley [d,e], Anka Bedetti [e], Peter Buss [f], Willem Frederik de Boer [g], Ellen S. Dierenfeld [h,i], Amanda Gardner [a], Simon C. Langley-Evans [b], Elliott Hamilton [a,b], R. Murray Lark [b], Herbert H.T. Prins [j], Anthony M. Swemmer [k], Michael J. Watts [a,*]

[a] Centre for Environmental Geochemistry, Inorganic Geochemistry, British Geological Survey, United Kingdom
[b] School of Biosciences, University of Nottingham, United Kingdom
[c] School of Veterinary Medicine and Science, University of Nottingham, United Kingdom
[d] Applied Behavioural Ecology and Environmental Research Unit, University of South Africa, South Africa
[e] Elephants Alive, Limpopo, South Africa
[f] Veterinary Wildlife Services, South African National Parks, South Africa
[g] Wildlife Ecology and Conservation Group, Wageningen University, the Netherlands
[h] Ellen S. Dierenfeld, LLC, Saint Louis, MO 63128, USA
[i] School of Animal, Rural & Environmental Sciences, Nottingham Trent University, United Kingdom
[j] Animal Sciences Group, Wageningen University, the Netherlands
[k] South African Environmental Observation Network (SAEON), Phalaborwa, South Africa

HIGHLIGHTS

- Home ranges of elephants around micronutrient hotspots were reduced.
- Overlap of micronutrient hotspots with activities such as mining causes conflicts.
- Influence of mineral provision must be considered when managing elephant populations.

GRAPHICAL ABSTRACT

Elephants on the Palabora Mining Company (PMC) land.

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ABSTRACT

The unique geochemistry surrounding the Palabora Mining Company (PMC) land may act as a micronutrient hotspot, attracting elephants to the area. The PMC produces refined copper and extracts phosphates and other minerals. Understanding the spatial influence of geochemistry on the home range size of African elephants is important for elephant population management and conservation.
The home ranges of collared elephants surrounding the PMC were significantly smaller ($P = 0.001$) than conspecifics in surrounding reserves, suggesting that their resource needs were met within these smaller areas. Environmental samples (soil, water and plants) were analysed from the mine area and along six transects radiating from the mine centre. Tail hair and faecal samples from elephants at the PMC, and conspecifics within the surrounding area were analysed. All samples were analysed for minerals essential to health and potentially toxic elements (PTEs; As, Ca, Cd, Cu, Fe, K, Mg, Mn, Na, P, Pb, Se, U, V and Zn). Results show that the geochemistry at the PMC is different compared to surrounding areas, with significant elevations seen in all analysed minerals and PTEs

* Corresponding author.
E-mail addresses: fsach@bgs.ac.uk (F. Sach), mwatts@bgs.ac.uk (M.J. Watts).

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Potentially toxic elements
Elephant movement

in soil closer to the mine, thereby drawing the elephants to the area. Additionally significant elevations were seen in elements analysed in water and vegetation samples. Elephant tail hair from elephants at the mine was significantly greater in Cd, whilst Mg, P, Cu, As, Cd, Pb and U concentrations were significantly greater in elephant faecal samples at the mine compared to the non-mine samples.
When micronutrient hotspots overlap with human activity (such as mining), this can lead to poor human-elephant coexistence and thus conflict. When managing elephant populations, the influence of mineral provision on elephant movement must be considered. Such detailed resource information can inform conservation efforts for coordinated programmes (UN SDGs 15 and 17) and underpin sustainable economic activity (UN SDG 8, 11 and 12).

1. Introduction

The increase in human population and global intensification of agriculture have significantly reduced African savanna elephant (*Loxodonta africana*) populations, through habitat reduction and fragmentation, causing the overlap of human and elephant habitation, leading to increased human-elephant conflict (HEC; Blanc, 2008). Elephants are forced into increasingly smaller areas, often restricted by fencing or encroaching anthropogenic activities, resulting in increased pressures on these areas to meet the elephants' resource needs. This can present nutritional challenges, resulting in altered elephant movement patterns and distribution in efforts to seek out required minerals. Elephants move to meet their mineral needs, and use available micronutrient hotspots, causing HEC, when these overlap with human activities (Sach et al., 2019). Minerals are required by elephants for a variety of biological processes including energy metabolism, organ and immune function, reproduction and cellular growth (Ishiguro et al., 2018).

Geochemistry influences mineral availability in soils, and thereby in plants and water to elephants (Prins and Langevelde, 2008). Understanding how the geochemistry of an area, and presence of micronutrient hotspots, influences mineral provision to the animal, informs how geochemistry influences home range size, especially when anthropogenic activities constrain long-distance movements. Largely, plants reflect the soil mineral profile, plants growing in deficient areas lack key minerals, which can result in deficiencies in the consumer (elephant). In contrast, plants growing in mineral rich areas pass on the mineral abundance to the consumer (Joy et al., 2015). Geochemical properties (including organic matter and soil pH), and the ability of plants to extract minerals from the soil will influence the availability of these minerals to elephants (Bowell and Ansah, 1994; Maskall and Thornton, 1996).

African elephants move and adapt their food selection, to meet their target levels of (as yet undetermined) minerals (Bax and Sheldrick, 1963). From here-on reference will be made to mineral in terms of the nutrient requirement for elephants. It is suspected that in volcanic areas such as the Palabora Mining Company (PMC), levels of micronutrients will be elevated, acting as a micronutritent hotspot, with a reduction in elephant home ranges size (Greyling, 2004). This may be beneficial or detrimental to elephants. In areas where the soil is generally deficient in minerals, it may allow elephants to meet their mineral needs within a small area. However, as with other mammals, dietary excess of minerals or potentially toxic elements (PTEs) can occur from overconsumption, causing toxic effects; data is limited as to these threshold levels for elephants (Sach et al., 2019). Elephants are large, slow-growing and can accommodate extended periods of nutrient deficiency due to their nutrient stores (Prins and Langevelde, 2008). Excess consumption of minerals or PTEs to harmful levels is likely to take several years (Ullrey et al., 1997).

As well as micronutrients, drivers for elephant movement include availability of food and water, social interaction, human activities, safety and access to shade (Wall et al., 2006). The distance travelled by elephants to meet their resource needs, will be reflected in their home range size (de Knegt et al., 2011). Mineral provision influences elephant food selections; for example, the Associated Private Nature Reserves (APNR), South Africa are suspected to have a localised phosphorus (P) deficiency, elephants increased their consumption of leaves from trees that had been fertilised with P (Pretorius et al., 2011, 2012). Secondly, females in family units maximised P intake by ingesting leaves with higher P content, to meet their increased requirements, compared to larger bodied males who consumed other lower P plant parts (Greyling, 2004). Phosphorus plays a role in reproduction and lactation (Groenewald and Boyazoglu, 1980). It is predicted that if an area such as the PMC is a micronutrient hotspot, elephants will remain within the locality, to meet their resource needs for minerals as demonstrated by Tucker et al. (2018), especially if the surrounding soils are poor in several essential micronutrients such as P, as suggested by Greyling (2004) and Pretorius et al. (2011, 2012).

The aim of this study was to understand the spatial influence of geochemistry on the home range size of elephants, using the Palabora Mining Company (PMC) property and surrounding national park land as a case study of contrasting environments. The following objectives were used to achieve the aim: (1) Determine if mineral levels in soil, forage and water near the mine are greater than the nearby Kruger National Park (KNP)/APNR and hence may influence a reduced elephant home range size; (2) Establish baseline levels for key minerals and PTEs in African elephant tail hair and faeces as potential biomarkers, and (3) Determine if the elephant tissues (tail hair and faecal samples) collected near the mine contain greater concentrations of essential minerals and PTEs, compared to elephants in surrounding reserves, away from the mine.

2. Materials and methods

The study was conducted on the Palabora Mining Company (PMC) land near Phalaborwa town, South Africa and adjacent areas within the KNP and the APNR (Fig. 1). From west to east, the geological succession of the KNP changes from granitic to basaltic. Granites generally form nutrient poor substrates whereas basaltic rocks form nutrient rich substrates (Venter and Gertembach, 1986). The APNR is located on the western border of the KNP, and is made up of gneiss, granite or magmatite (Venter and Gertembach, 1986). Elephants can move freely amongst the KNP, APNR and PMC lands. Elephant incursion into the PMC can cause financial losses and risk to elephant and human life. Elephants can damage infrastructure, inhibit mining operations and cause elephant, vehicle and train collisions.

In this generally micronutrient poor environment, the Palabora Igneous Complex has a unique mineral rich rock formation. Commercial mining began in 1954, with open-cast mining of foskorite and pyroxenite, thereafter the PMC began mining the same ores for copper and magnetite, developing into the country's main producer of refined copper, operating over 1950 ha (Roux et al., 1989). The NGO Elephants Alive (EA) have collared elephants throughout the APNR, and seven elephants utilising the mine area (movements in Fig. 2). The home range of these mine collared elephants was calculated using a-LoCoH 90% (Getz and Wilmers, 2004), and was smaller than that of neighbouring elephants within the APNR (Table 1), animals of the same sex, age

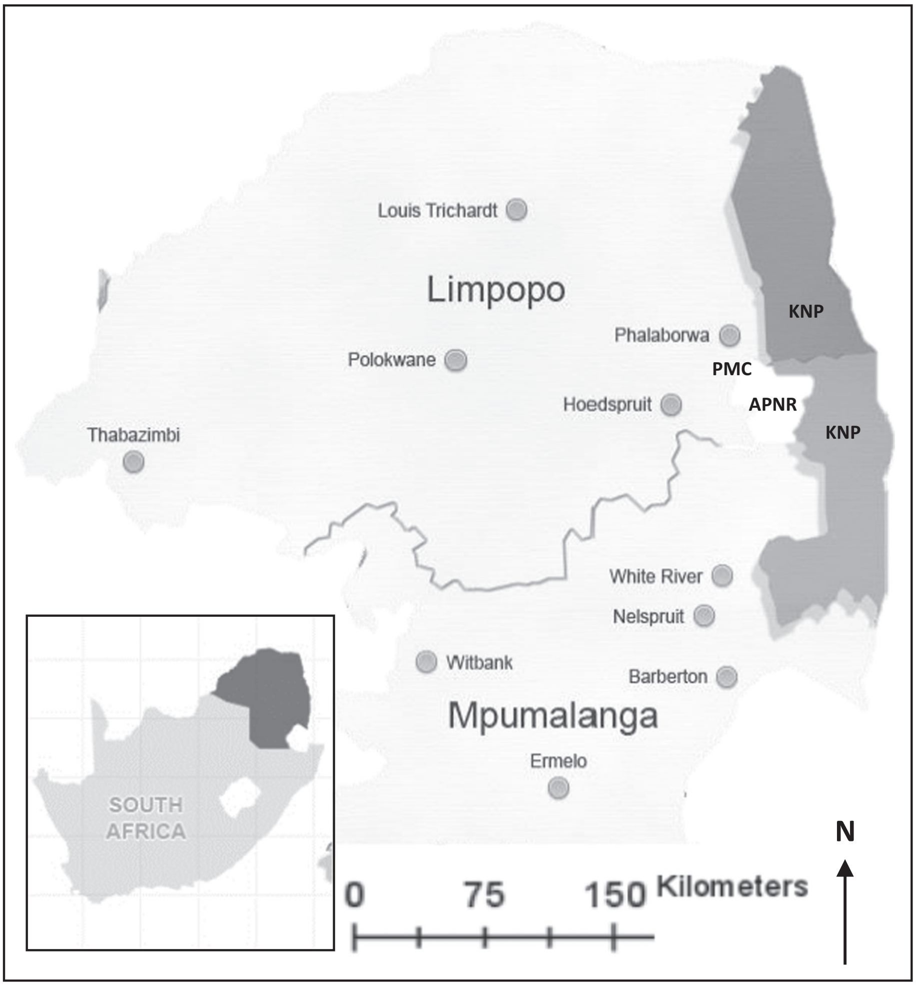


Fig. 1. Study area showing the Kruger National Park (KNP), Associated Private Nature Reserves (APNR) and Palabora Mining Company (PMC).

category and wearing collars for the same time period were compared. Elephant census data, showed that elephant density within the operational PMC (1.4 per km^2) was larger than that within the surrounding KNP (0.8 per km^2; Lerm and Swemmer, 2015).

2.1. Sample site selection

Fifty-three sampling sites were selected on six transects radiating out from the PMC, to include points within and outside of the area occupied by the collared elephants at the mine (Fig. 3). Transects were used to observe if an elemental gradient from the PMC was present. Additionally, 43 sampling sites were identified within the PMC (Fig. 3). Sample sites were not selected to the north west of the PMC area, this is a fenced urban area with minimal elephant movement.

2.2. Sample collection

Environmental and faecal sampling was conducted during September 2017 and September 2018, within a 50 m radius around each sampling point. Trace element free paper bags were used for plant, soil, faecal and tail hair samples. All samples were transported to the lab within 8 h of collection; plant and water samples in a cooler, tail hair, faecal and soil samples at ambient temperature.

2.3. Environmental sampling

Plant parts (approx. 500 g per sample, $n = 100$) were sampled from seven species commonly consumed by elephants (Table 2; Smallei and O'Connor, 2000; Holdø et al., 2002; Codron et al., 2006; Pretorius et al., 2011, M Henly pers. comm 2017). Not every species or part was found at the sampling site. Samples were taken randomly from the plant, mixed sized leaves were sampled, branches/roots of approx. 5 cm in length were cut using secateurs and bark was scraped off the trunk using a chisel.

Soil samples (n = 97, approx. 500 g per sample) were collected at each site, from surface soil using a trowel, to a depth of 15 cm, from five separate points within a 1-m^2 grid. Water was sampled opportunistically at sample sites, key rivers or identified elephant drinking points ($n = 36$); two 30 ml samples were collected in Nalgene HDPE bottles, filtered (0.45 μm).

2.4. Biological sampling

Elephant faecal samples ($n = 94$, approx. 500 g per sample) were taken from the centre of fresh, intact boluses with circumference of >40 cm, to indicate adult size (Jachmann and Bell, 1985), as calf samples on a pre-weaned diet could bias results (Cook et al., 1994). On return to the laboratory, samples were oven dried at 50 °C for 24 h.

Tail hair samples were plucked from the tail (1–3 hairs per animal) between March 2002 and July 2018 during routine collaring operations or management activities throughout the KNP, APNR and PMC, as part of the South African National Parks Bio-bank (SANParks), or by EA. Tail hair samples were taken up to 170 km from the PMC ($n = 200$ from non-mine collected by SANParks and EA, $n = 7$ from mine area collected by EA). All sedations

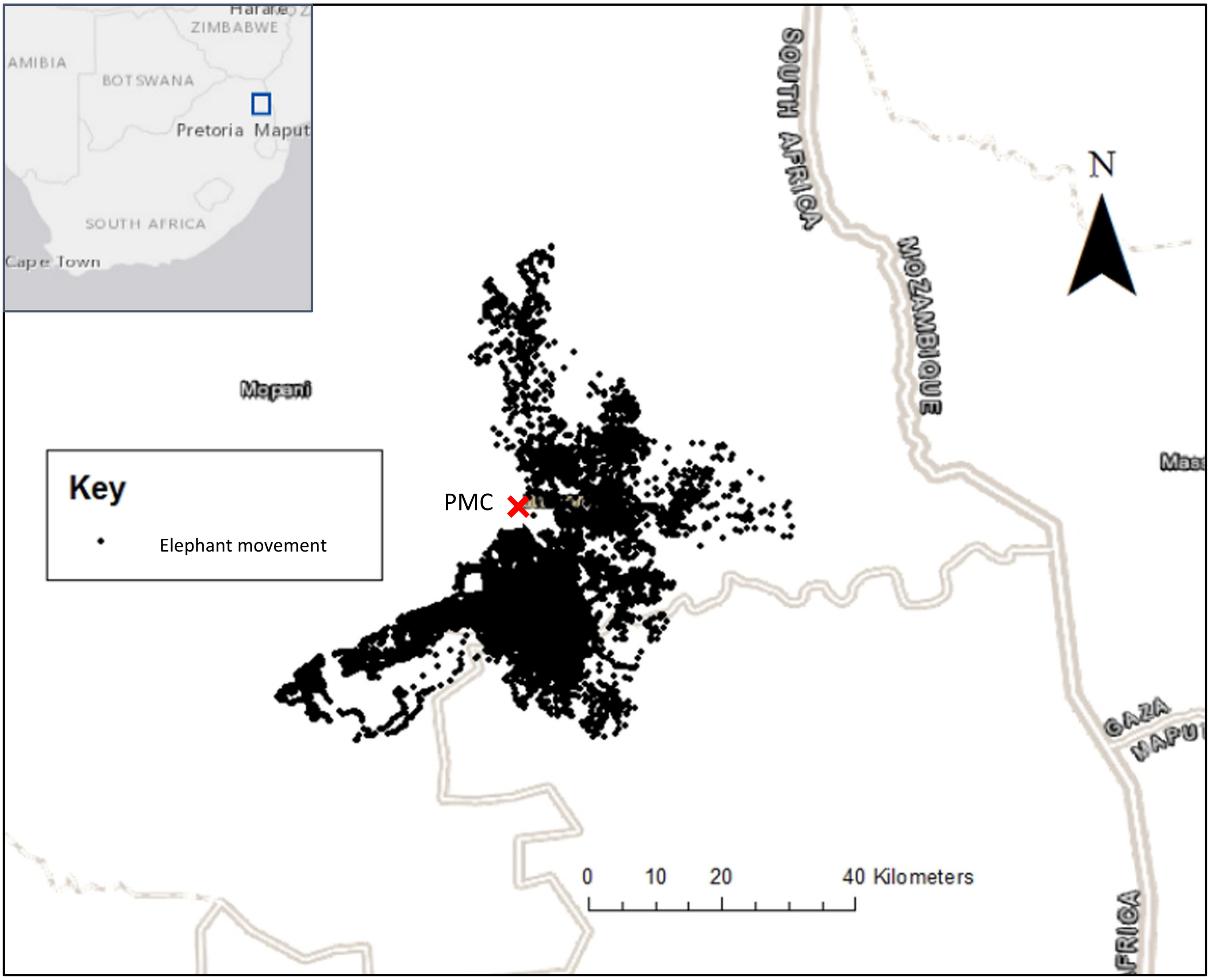


Fig. 2. Fixes of collared elephants surrounding the Palabora Mining Company (PMC) site between 15.6.2012 and 23.7.2017.

were carried out using the SANParks SOPs for Capture Transport (*Standard Opperating Procedures for Capture Transport and Maintenance in Holding Facilities of Wildlife*, 2017).

2.5. Sample preparation

Soil samples were air-dried, crushed and sieved to ≤2 mm particle size and further milled to ≤40 μm in an agate ball mill. Water samples were filtered with a hydrophilic 25 mm Minisart filter and acidified to 1% HNO_3 and 0.5% HCl. Plant and faecal samples were oven dried at 50 °C for 24 h, and passed through a food blender as described by Watts et al. (2019). Elephant tail hair samples were cleaned as described in Middleton et al. (2016) and autoclaved in line with DEFRA requirements.

2.6. Sample digestion for ICP-MS analysis

Soil samples (0.25 g) were digested in a mixed acid solution (HF: 2.5 ml/HNO_3:2 ml/$HClO_4$:1 ml/H_2O_2:2.5 ml) on a programmable hot block; 0.5 g of plant samples or faecal samples were digested in HNO_3:10 ml/H_2O_2:1 ml mixed solution in a closed vessel microwave heating system (MARS Xpress) as described in Watts et al. (2019). Elephant tail hair samples (variable weight) were digested in HNO_3:4 ml/H_2O_2:1 ml mixed solution in a closed vessel microwave heating system (MARS Xpress) as described in Middleton et al. (2016). Tail hairs from the non-mine elephants were digested and analysed whole, and those from the collared elephants at the PMC were cut into 3–5 cm sections, down the length of the hair, for future profiling, prior to digestion and subsequent analysis. Soil, plant, faecal material and tail hair data is presented as dry weight.

Table 1
Home ranges of elephants within the Palabora Mining Company (PMC) land and neighbouring reserves. Full data given in Supplementary Information Table 9.

	Average home range calculated using LoCoH 90% (km^2)	Standard error of mean	Min/max (km^2)	Number of elephants
PMC	529	78	200/728	7
Neighbouring reserves	1305	265	498/2244	7

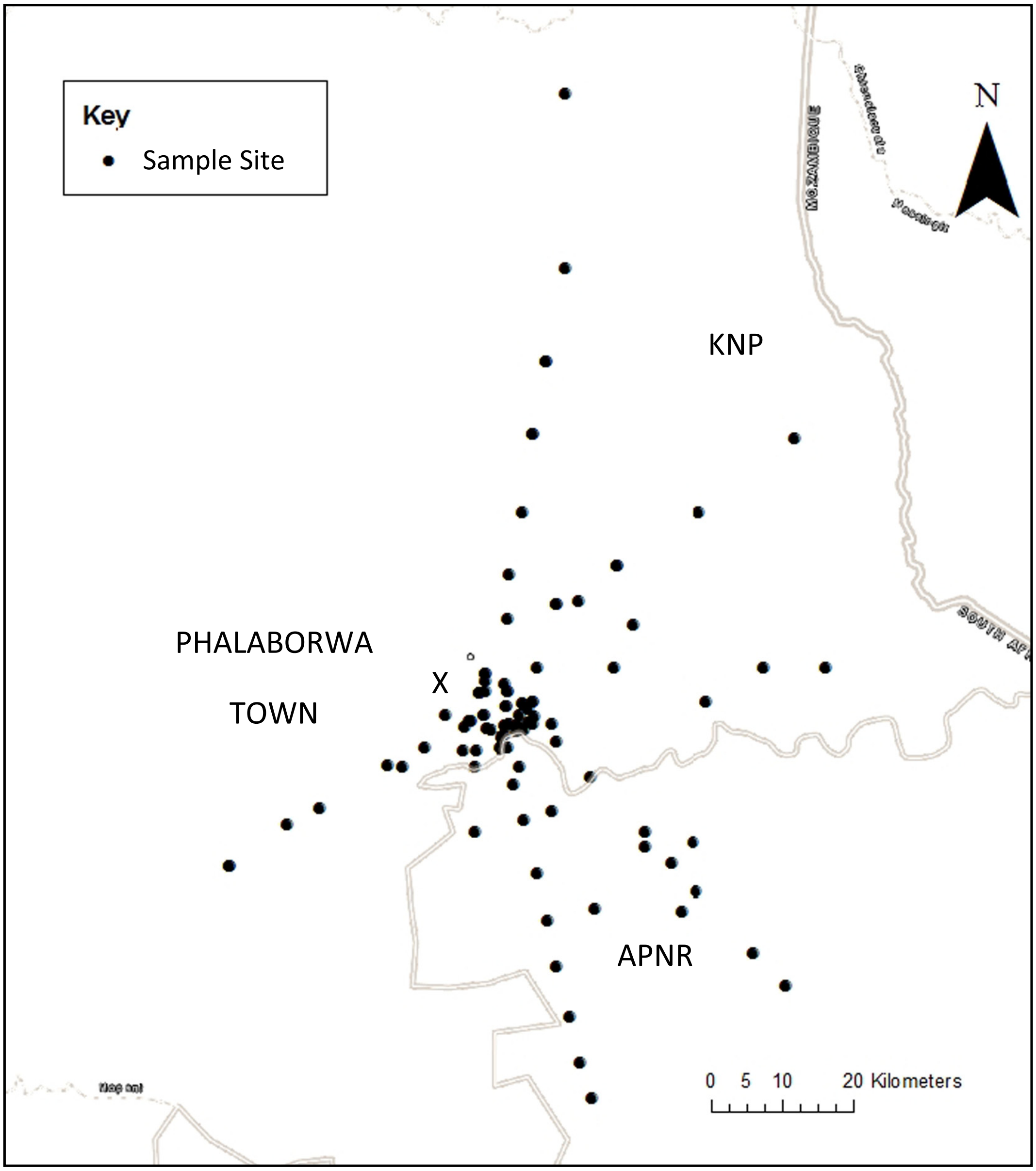


Fig. 3. Sampling sites for environmental and faecal samples. KNP=Kruger National Park; APNR = Associated Private Nature Reserves. The PMC (Palabora Mining Company) is located where transects cross, south of Phalaborwa town.

2.7. Elemental analysis

Elemental analysis was conducted on all prepared samples by inductively coupled plasma mass spectrometry (ICP-QQQ; Agilent 8900×) using collision cell mode (gas modes: H_2 for Se, O_2 for As, He for all remaining elements). Fifteen biologically functional or potentially toxic elements were selected for this study; Ca, copper (Cu), iron (Fe), potassium (K), Mg, manganese (Mn), Na, P, selenium (Se), zinc (Zn), arsenic (As), cadmium (Cd), lead (Pb), uranium (U) and vanadium (V). Sample blanks were run to determine the practical limit of detection (LOD, 3*STDEV).

Table 2
Plant species and plant parts sampled within this study.

Species	Common name	Part sampled
Colophospermum mopane	Mopane	Leaves
Grewia monticola	Silver Raisin	Bark
		Leaves
Senegalia nigrescens	Knob Thorn	Bark
Combretum apiculatum	Red Bushwillow	Roots
Lannea schweinfurthii	False Marula	Leaves
		Inner bark
Dichrostachys cinerea	Sicklebush	Branches
		Leaves
Maerua parvifolia	Dwarf Bush-cherry	Branches
		Bark
		Leaves

2.8. Analytical quality control

The accuracy of the elemental analysis was verified by analysing the following certified reference materials (CRM)s:

- Human Hair (GBW07601, China)
- Spinach leaves (SRM1570a, NIST, USA)
- Tomato leaves (SRM1573a, NIST, USA)
- Basalt rock (BCR-2 United States Geological Survey, USA)
- Soil (SRM2711a, NIST, USA)

- Soil (BGS 102, British Geological Survey, UK)
- In house human toenail (BAPS 2014) reference material

The concentrations of all elements of interest in the reference materials had an acceptable accuracy to the target values, of 97% ± 39%, data detailed in Supplementary Information Table 3.

2.9. Statistical analysis

The evidence for differences between mine and non-mine elephant home range size was assessed by a Wilcoxon-test of the null hypothesis that the median home range size value was the same for the collared mine and non-mine elephants. Statistical analysis was conducted using 'R' Studio version 3.5.0.

The evidence for differences between mine and non-mine elephant tail hair and faecal samples with respect to analytes was assessed by a Student's *t*-test of the null hypothesis that the mean value was the same for samples from the mine and non-mine. Boundaries to define the mine and non-mine were based on physical land ownership. The *t*-test was performed assuming that the variances within the two groups were not necessarily the same, and computing effective degrees of freedom for the resulting t-statistic according to the Satterthwaite-Welch equation (Welch, 1947). This is a conservative approach when, as here, the sample sizes are unequal.

Each family of tests (*t*-tests on one matrix for the set of minerals, or tests of trend models for some environmental matrix on the set of minerals) can be regarded as a multiple hypothesis testing exercise, because each mineral was not considered in turn, but rather examined for evidence that specific minerals display behaviour of interest. For that reason we undertook false discovery rate control (FDR) following Benjamini and Hochberg (1995). The FDR is the expected proportion of rejected null hypotheses that should have been accepted. Here we controlled the FDR at 0.05, computing adjusted *P*-values for each family of tests using the p.adjust command in the base statistical library of the R package (R Core Team, 2017).

The environmental data, on soil, water and plants, were examined for evidence that there is a dependency of the measured concentration on distance from the mine. This was done using a polynomial function of distance. For plants, leaves only were used to demonstrate spatial variation, a full dataset and comparison for the plant data (all plants versus leaves) is in Supplementary Information Table 4. The data on soil, water and plants were collected from transect points radiating from the mine, sampling at more or less regular intervals. Because the samples are not collected from sites selected independently and at random, it is not possible to make sound inferences based on standard ordinary least squares methods (Lark and Cullis, 2004). Rather, it is necessary to fit a linear mixed model (LMM) to the data, with the fixed effects comprising polynomial terms in distance to the mine, and the random effect comprising both an independent and identically distributed error term and a spatially correlated random effect. The models were fitted using the lme and update functions from the nlme library for the R platform (R Core Team, 2017; Pinheiro et al., 2018).

A quartic polynomial (first, second, third and fourth order terms) in distance was initially fitted to the data by ordinary least squares, and summary statistics and the histogram of the residuals were examined to decide whether to analyse the data on their original units or after transformation to natural logarithms. The full model was then fitted as a LMM using residual maximum likelihood (REML), and models with spherical and exponential correlation functions for the spatially-dependent random effect were compared on their likelihood. The selected spatial correlation function was then retained for all further models for this variable on the matrix being considered. The full quartic model was then re-estimated using ordinary maximum likelihood to allow comparisons with alternative models with different fixed effects. A cubic model was then fitted (i.e., dropping the quartic term), and the quartic and cubic models were compared on the log-likelihood ratio statistic to test the null hypothesis that the coefficient for the quartic term was zero. If this null hypothesis was rejected then the full model was retained and compared with a null model in which the only fixed effect was a constant mean. This latter test was recorded as the strength of evidence for a trend with distance to the mine. If, on the other hand, the null hypothesis was accepted, then the quartic term was dropped and the cubic model compared with a quadratic, and so on.

As with the comparisons between the mine and non-mine areas by the *t*-test, each set of spatial models over all elements on a particular matrix was treated as a family of multiple hypotheses to be tested with FDR control. The same method was used to do this as described above for the *t*-tests.

One data point furthest from the mine was removed, because of the considerable leverage that this could have on a trend model. It was also necessary to "jitter" some of the spatial coordinates, moving them 1 m in a random direction. This is because, although none of the environmental samples on any matrix were actually from the same location, the GPS coordinates were duplicated as GPS readings are only precise within 6 m. It was one observation out of any such pair that was "jittered" in this way using the jitterDupCoords function from the geoR package in R (Ribeiro and Diggle, 2018).

2.10. Statement of ethical approval

Required ethical clearance and permits were obtained from relevant authorities.

3. Results

3.1. Home range size

The null hypothesis that the mean home range size was the same for the mine and non-mine areas could be rejected. The Wilcoxon test showed a significant difference between mine and paired conspecifics outside of the mine ($P = 0.001$; Table 1; Supplementary Information Table 9).

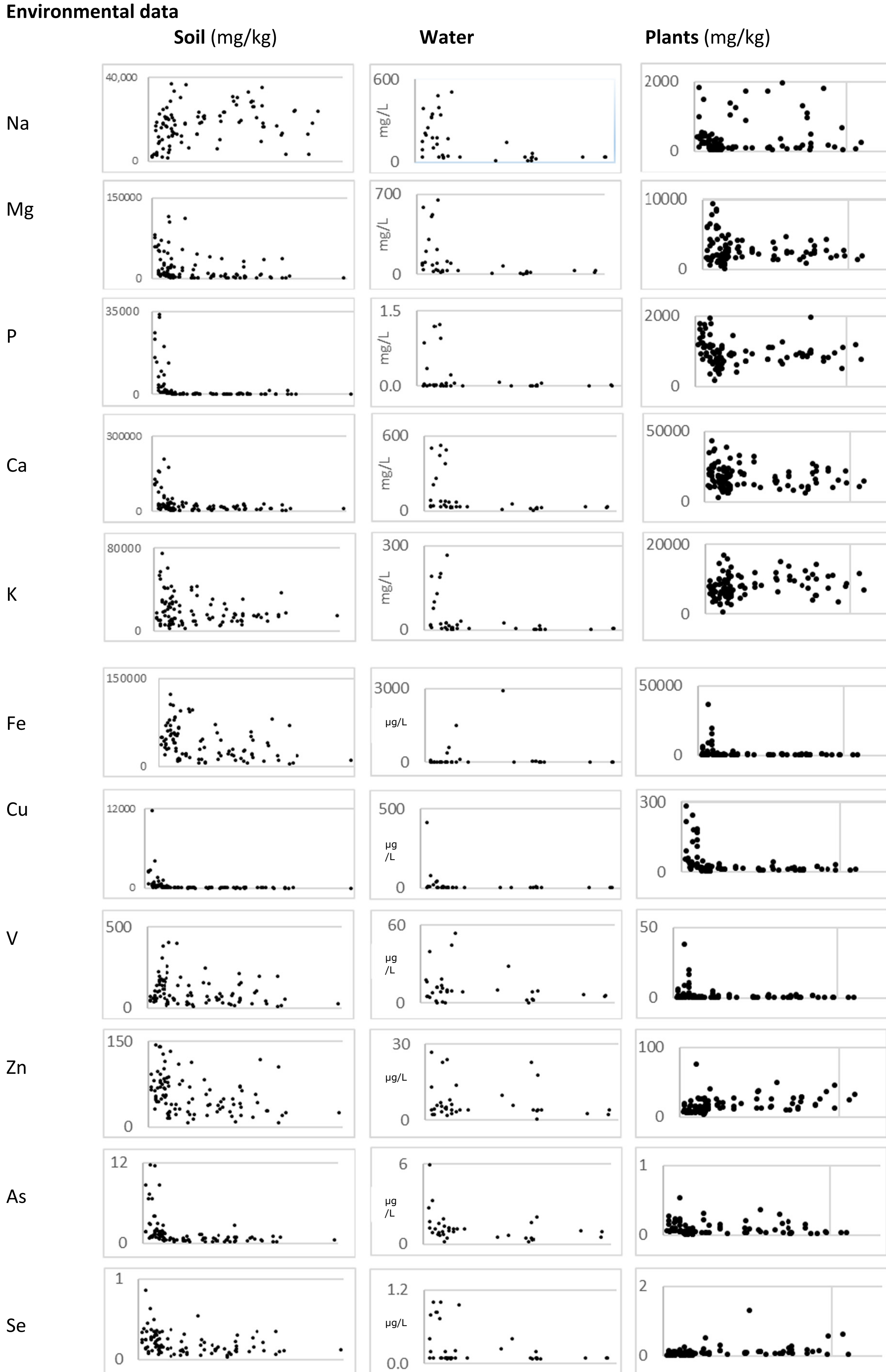
3.2. Environmental samples

With FDR control at 0.05, the null hypothesis of no spatial trend in concentration in the soil with distance from the mine could be rejected for all investigated elements. Inspection of the trend model shows that in all cases concentrations decline with distance (Fig. 4; Table 3; Supplementary Information Tables 3 and 8). With FDR control at 0.05, the null hypothesis of no spatial trend in concentration in the water with distance from the mine could be rejected for four investigated elements (Ca, K, Fe and Cu), with concentrations declining with distance (Fig. 4; Table 3; Supplementary Information Tables 5 and 8). With FDR control at 0.05, the null hypothesis of no spatial trend in concentration in plants (leaf samples) with distance from the mine could be rejected for nine investigated elements (P, Mg, Mn, Fe, Cu, Zn, Se, Cd, and U), with concentrations declining with distance (Fig. 4; Table 3; Supplementary Information Tables 4 and 8).

3.3. Elephant biomarkers

With FDR control at 0.05, the null hypothesis of no difference between the mine and non-mine faecal samples could be rejected for Mg, P, Cu, As, Cd, Pb and U (larger concentrations in the elephants near the mine) and Na, Mn, Zn and Se (smaller concentrations in the elephants near the mine; $P < 0.05$; Fig. 5; Supplementary Information Tables 7; 8).

With FDR control at 0.05, the null hypothesis of no difference between the mine and non-mine tail hair samples could be rejected for



Environmental data
Soil (mg/kg)
Water
Plants (mg/kg)
Na
40,000
0
600
mg/L
0
2000
0
Mg
150000
0
700
mg/L
0
10000
0
P
35000
0
1.5
mg/L
0.0
2000
0
Ca
300000
0
600
mg/L
0
50000
0
K
80000
0
300
mg/L
0
20000
0
Fe
150000
0
3000
μg/L
0
50000
0
Cu
12000
0
500
μg
/L
0
300
0
V
500
0
60
μg
/L
0
50
0
Zn
150
0
30
μg/L
0
100
0
As
12
0
6
μg
/L
0
1
0
Se
1
0
1.2
μg/L
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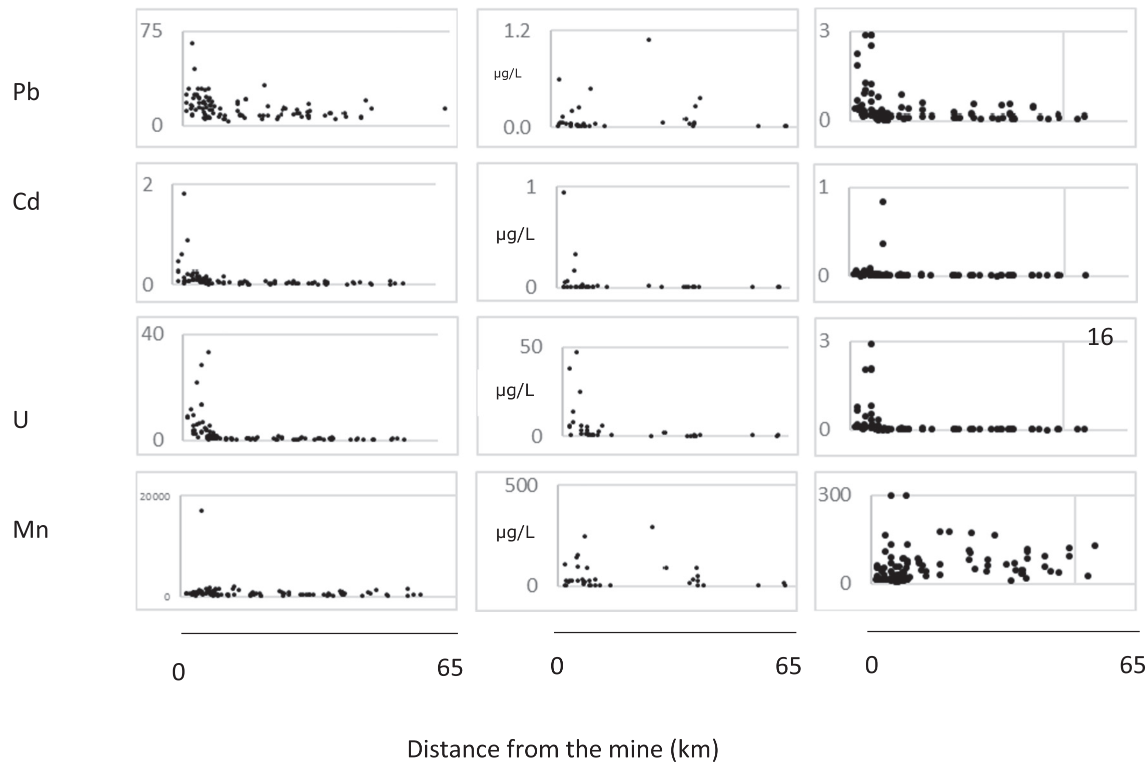

Fig. 4. Overview of elemental analysis of environmental samples (y-axis), against distance from the mine (x-axis). Plant data = median of all samples collected (leaves, twigs and branches).

Cd (larger concentrations in the elephants near the mine) and K and Se (smaller concentrations in the elephants near the mine; $P < 0.05$; Fig. 5; Supplementary Information Table 6s; 8).

4. Discussion

Mineral provision at the PMC was greater than the surrounding areas (Table 3; Fig. 4). Home ranges of the mine elephants were significantly smaller (59% $P = 0.001$) than those in the surrounding areas (Fig. 2; Table 1), suggesting that their resource needs, including minerals, were met within this smaller area, close to the PMC (Tucker et al., 2018). A trade-off is likely whereby elephants consume soil and water (or plants) near the PMC to obtain increased levels of Ca, Mg, P, Cu, Zn and Se but also consume PTEs (Pb, U and V). Selenium and Zn are fertility augmenters, benefiting elephants in early life (Hidiroglou and Knipfel, 1984; Mistry et al., 2012), whereas the effects on fertility from consuming PTE's to toxic levels may take decades to realise, having a lesser effect on total reproductive output (Kincaid, 1999). An evolutionary advantage may be gained in consuming increased micronutrients at the PMC, at the cost of the increased consumption of PTEs. High consumption of macro-minerals (seen in plants) are under homeostatic control within the elephant, and thus the elephant can buffer increased intake (Kincaid, 1999).

4.1. Biological samples

Tail hair reflects up to 18 months residence, whereas faecal material reflects short-term dietary intake (Bencko, 1995; Wittemyer et al., 2009). The differences in tissue biomarkers indicated that short-term environmental differences in availability of minerals consumed by the elephants, appeared to be reflected directly by faecal samples. Whereas, the tail hair data suggested that the elephants moved to obtain required minerals over time, thereby not showing significant differences in as many elements, between mine and non-mine samples (11 of 15 elements in faecal material versus 3 of 15 elements in tail hairs). Such temporal variability must be considered in evaluating the use of biomarkers for assessing nutrient status/habitat quality.

This study covers the widest range of minerals and PTE analysis in elephant faeces to date ($n = 97$; Fig. 5; Supplementary Information Table 7). In Hwange National Park, Zimbabwe, Mg, Na and K data were similar to concentrations found in this study (Holdø et al., 2002). However, in this study, faecal Ca concentrations, both from mine and non-mine samples were substantially larger than reported by Holdø et al. (2002) with the minimum and maximum level in this study being 8100 and 23,100 mg/kg DM, respectively, versus 920 and 12,000 mg/kg DM. Additionally, in the APNR, Greyling (2004) reported similar P levels in faecal samples (median 1100 versus 990 mg/kg DM in this study). Faecal samples reflect Ca intake (Sach et al., 2020), therefore increased Ca levels found in in this study could be attributed to increased intake.

Faecal samples may not represent a specific location or plant consumed; elephants have a total gut transit time of 11–46 h (Clauss et al., 2003) and walk over 22 km daily (Thomas et al., 2012). Faecal samples were a reliable indicator of Ca, P, Se, Cu and As intake (Sach et al., 2020) and thus a proxy for elemental status. Significantly greater levels of faecal P, Cu and As were seen in mine samples compared to non-mine samples, indicating that intake of these elements were greater in mine versus non mine. This is also seen in soil, in Cu in water and P and Cu in plants (leaves), supporting this increased intake. Additionally, elephants are frequently documented to participate in geophagy (Holdø et al., 2002), and although not specifically reported at PMC, could be in part obtaining these increased elemental levels via geophagy.

This study provides the largest multi-element dataset on mineral and PTE analysis data in elephant tail hair (Fig. 6; Supplementary Information Table 6). Hair analysis is routinely used in humans and livestock to assess Se and As levels (Bencko, 1995; Middleton et al., 2016). Duer, Tomasi and Abramson, (2016) analysed an elephant tail hair from a deceased healthy individual from Tsavo National Park, Kenya and reported 11 elements for which concentrations were comparable to the non-

Table 3
Results of linear mixed model to show significant differences in soil, water and plant (leaf) concentrations as distance from the mine increased. *P*-value (<0.05) represented as bold text in the table and adjusted *P*-values to control the false discovery rate (FDR) reported.

	Soil		Water		Plants/leaves	
Element	P-value	Adjusted P-value	P-value	Adjusted P-value	P-value	Adjusted P-value
Ca	**0.05**	**0.043**	0.42	**0.038**	0.336	0.360
l ratio	5.84		0.65		0.926	
Number	2		1		1	
P	<**0.0001**	**0.000**	**0.03**	0.060	<**0.0001**	**0.005**
l ratio	40.27		4.82		19.52	
Number	4		1		4	
Mg	<**0.0001**	**0.000**	**0.02**	0.075	<**0.0001**	**0.005**
l ratio	31.88		5.42		68.08	
Number	4		1		2	
Na	**0.04**	**0.050**	**0.01**	0.525	0.5317	0.532
l ratio	4.44		6.05		1.26	
Number	1		1		2	
K	**0.04**	**0.043**	**0.01**	**0.038**	0.33	0.360
l ratio	4.44		7.88		0.93	
Number	1		1		1	
V	**0.002**	**0.003**	0.31	0.423	0.10	0.136
l ratio	9.18		1.02		4.60	
Number	1		1		2	
Mn	**0.001**	**0.002**	0.60	0.692	<**0.0001**	**0.020**
l ratio	10.47		1.86		6.9662	
Number	1		3		1	
Fe	**0.0003**	**0.001**	<**0.0001**	**0.000**	**0.03**	**0.050**
l ratio	12.94		42.50		6.77	
Number	1		1		2	
Cu	**0.009**	**0.012**	**0.01**	**0.038**	**0.01**	**0.021**
l ratio	9.42		8.78		8.68	
Number	2		2		2	
Zn	**0.02**	**0.025**	0.96	0.960	**0.003**	**0.009**
l ratio	7.96		0.00		8.78	
Number	1		2		1	
As	<**0.0001**	**0.000**	0.16	0.267	0.30	0.360
l ratio	47.96		1.95		3.66	
Number	2		1		3	
Se	**0.00**	**0.008**	0.11	0.206	**0.02**	**0.038**
l ratio	9.60		2.51		5.65	
Number	1		1		1	
Cd	<**0.0001**	**0.000**	0.08	0.171	<**0.0001**	<**0.0001**
l ratio	51.20		0.08		25.54455	
Number	2		1		1	
Pb	<**0.0001**	**0.000**	0.77	0.825	**0.04**	0.060
l ratio	114.46		0.08		6.24	
Number	1		1		2	
U	**0.002**	**0.003**	0.26	0.390	**0.0027**	**0.009**
l ratio	14.44		1.28		11.84	
Number	3		1		2	

mine elephants within this study. However, levels of Mg, Ca, Mn, Cu and Pb in the mine elephant tail hairs were considerably greater than those reported by Duer et al. (2016).

4.2. Environmental samples

This study agrees with work reported by Ramahlo (2013) within the Phalaborwa region, regarding the impact of mining on soil at surrounding farms, where P, As and Pb levels in soil decreased with increasing distance from the mine. African soils contain high levels of Fe (Siyame et al., 2013), and thus a significant difference between mine/non-mine faecal or tail hair samples may not be seen (Figs. 5 and 6), as all animals may be consuming to excess. Studies demonstrated elephants selectively drank water with elevated mineral levels; notably Na, iodine (I), sulphur (S), Zn, Ca, Mg, Mn and Fe (Weir, 1972; Sienne et al., 2014). Additionally, elephants may spend more time at the PMC site during the dry season, either due to mineral deficiencies in natural forage being heightened in the dry season, or simply for increased water availability within the PMC area (Purdon and van Aarde, 2017).

Elemental analysis of plant samples do not always reflect soil due to a variety of factors including soil pH, organic matter and differences in the capacity of individual plant species to accumulate certain elements (Bowell and Ansah, 1994; Maskall and Thornton, 1996). In the Sabi Sands Reserve, South Africa, grasses were analysed from soils of higher mineral levels, yet they accumulated less minerals compared to grasses from soils where the minerals were lower (Ben-Shahar and Coe, 1992), due to differences in soil-to-plant transfer between plant species and the effect of the local micro-climate. Similarly, this variation in soil-to-plant transfer was reflected in this study for Ca, Na, K, V, As and Pb (Fig. 4; Table 3). These elements decreased significantly in soil with distance from the mine, although plants did not follow the same trend. The igneous Phalaborwa apatite would be expected to have low reactivity (i.e. low solubility), hence the elements in the soil may be less available for uptake by plants (Appleton, 2002). Finally high soil Fe, typical of African soils, could also reduce the availability of P to animals via plants, thus the increase in soil P may not be reflected within mine tail hair samples (Fordyce et al., 1996).

5. Conclusion

The home ranges of the collared PMC elephants are considerably smaller (59% smaller) than elephants in surrounding areas, implying that their resource needs are being met within this relatively compact area. Drivers for elephant movement are multifactorial, yet evidence suggests that these key differences in the geochemistry of the mine compared to the surrounding areas, could act as a driver for elephant movement, resulting in reduced home range size compared to other elephants within this geographical region. Mineral provision to the elephants at the PMC is significantly greater than in surrounding areas, seen most significantly in the soil where all investigated mineral and PTE levels decreased significantly with increasing distance from the mine. These differences suggest that elephants are attracted to this micronutrient hotspot at the PMC, to obtain required minerals.

The increased mineral provision and trade off of increased PTE levels were reflected in biological samples of elephant tail hair and faeces. Baseline levels of key minerals and PTEs in African elephant tail hair and faeces were established from this work. The methods described within this natural experiment to investigate how environmental geochemistry influences elephant home range size and potentially movement, facilitates the consideration of intervention to reduce associated HECs at the PMC. This approach could be applied to similar situations, with wider benefits to a variety of stakeholders, informing broader conservation efforts.

CRediT authorship contribution statement

Fiona Sach: Conceptualization, Methodology, Data curation, Investigation, Formal analysis, Writing - original draft. **Lisa Yon:** Conceptualization, Methodology, Writing - review & editing. **Michelle D. Henley:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing. **Anka Bedetti:** Data curation, Writing - review & editing. **Peter Buss:** Investigation, Resources, Writing - review & editing. **Ellen S. Dierenfeld:** Conceptualization, Methodology, Writing - review & editing. **Amanda Gardner:** Investigation, Writing - review & editing. **Simon C. Langley-Evans:** Conceptualization, Methodology, Supervision, Project administration, Writing - review & editing. **Elliott Hamilton:** Investigation, Formal analysis, Writing - review & editing. **R. Murray Lark:** Formal analysis, Writing - review & editing. **Anthony M. Swemmer:** Conceptualization, Methodology, Resources, Writing - review & editing. **Michael J. Watts:** Conceptualization, Funding acquisition, Project administration, Validation, Methodology, Resources, Supervision; Writing - review & editing.

Biological data

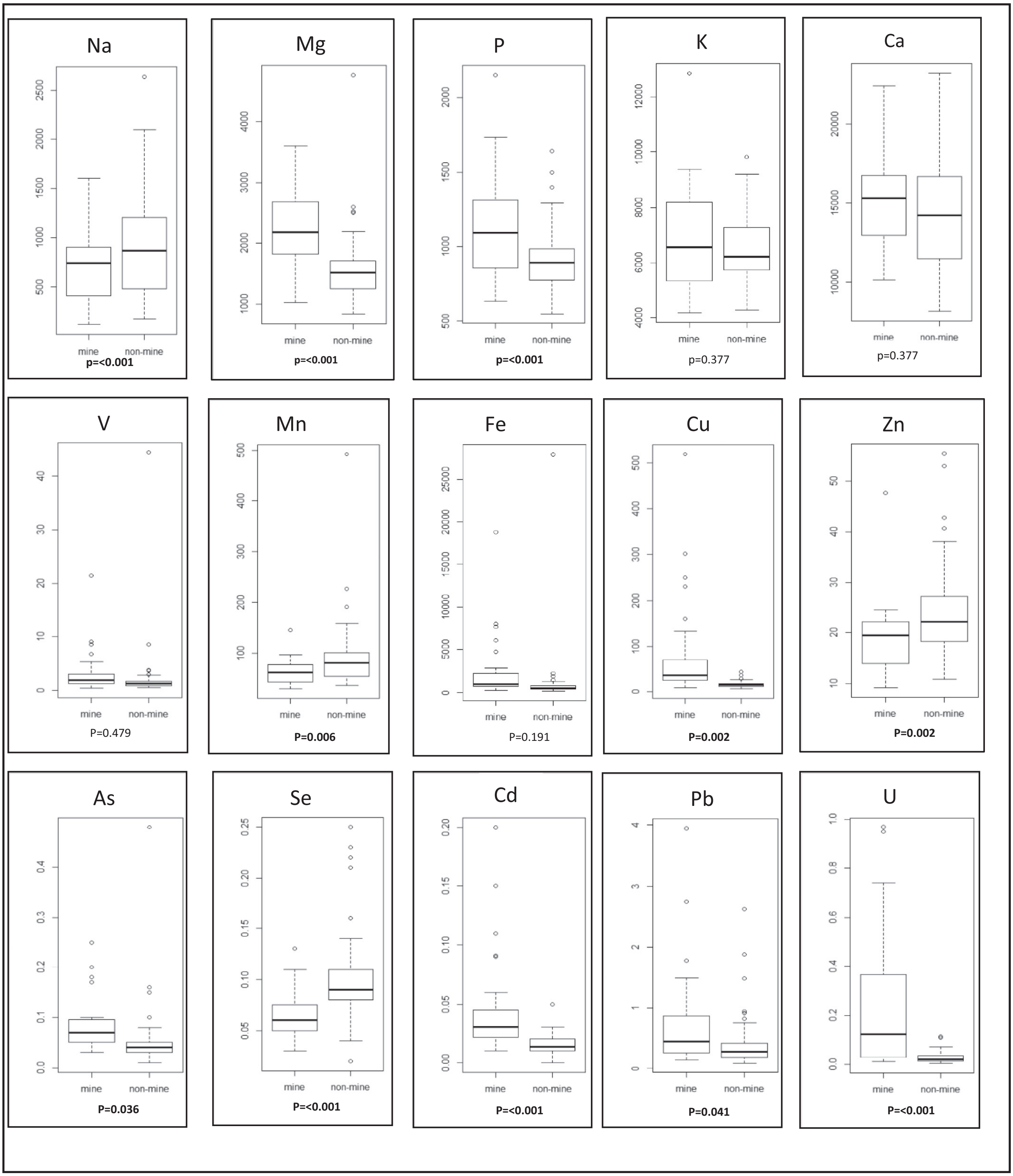

Fig. 5. Elemental analysis data (y-axis, mg/kg) for faecal samples. Box plots show median, Q2, Q3, max and min. Outliers are defined as 1.5*IQR. Adjusted P-values are reported to control for false discovery ($p < 0.05$). For mine samples $n = 37$, non-mine $n = 57$.

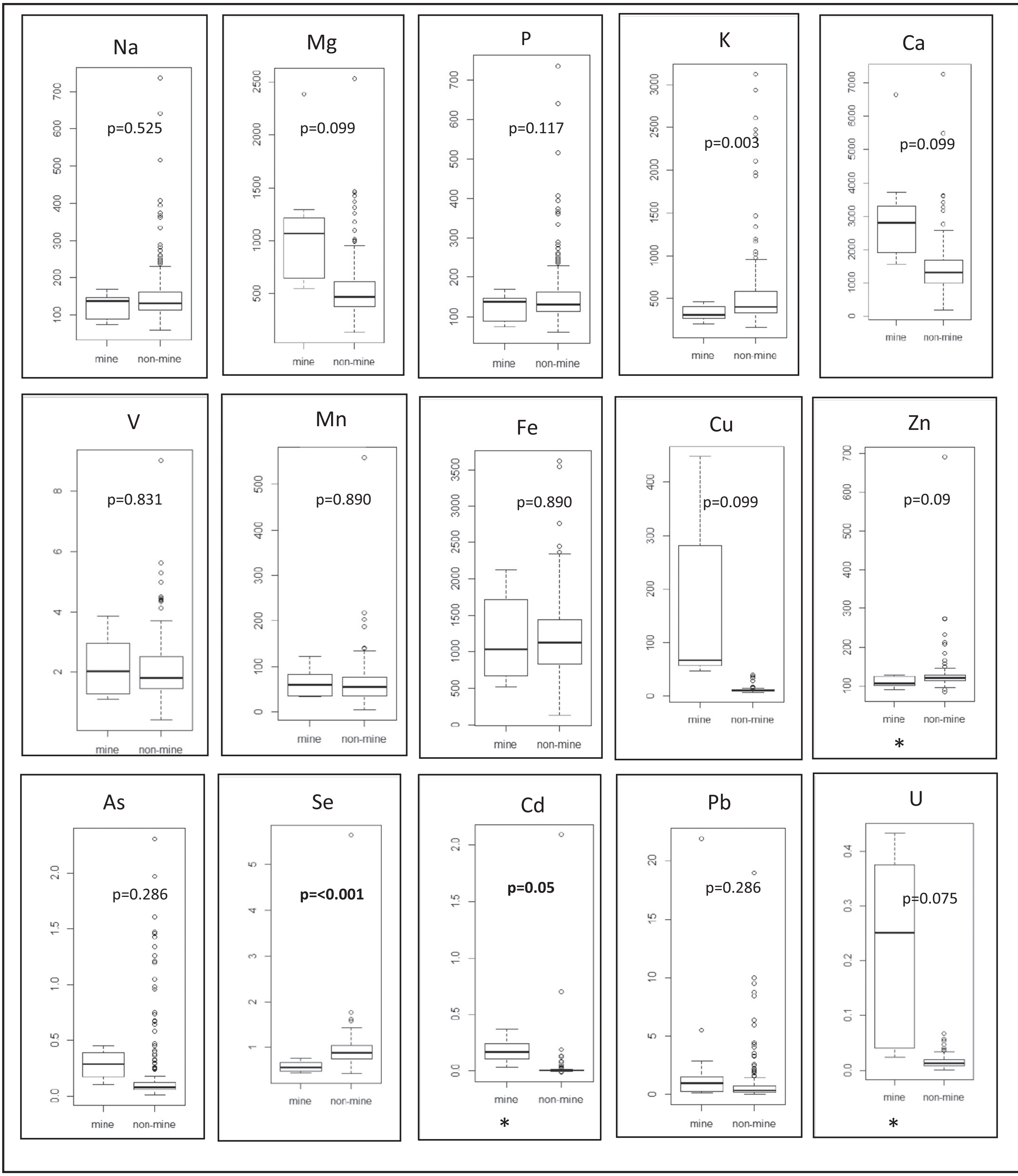

Fig. 6. Elemental analysis data (y-axis mg/kg) from tail hair samples from mine and non-mine elephants, y axis = element concentration (mg/kg). Box plots show median, Q2, Q3, max and min. Outliers are defined as 1.5*IQR. Adjusted *P*-values are reported to control for false discovery ($p < 0.05$). For mine samples n = 7, for non-mine samples $n = 200$.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ellen Dierenfeld is employed by Ellen Dierenfeld Consulting LLC.

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Appendix A. Supplementary data

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