Received: 4 January 2021 | Revised: 21 April 2021 | Accepted: 18 June 2021

DOI: 10.1111/aje.12907

SHORT COMMUNICATION

African Journal of Ecology WILEY

Hyaenas play unique ecosystem role by recycling key nutrients in bones

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Funding information
Tswalu Foundation

1 | INTRODUCTION

Bones contain significant levels of calcium (Ca) and phosphorus (P), which are important to the functioning of terrestrial ecosystems (Carter et al., 2007). Both minerals are essential for cellular processes and structures and can limit the growth and reproduction of plants and animals (Schlesinger & Bernhardt, 2013). Accordingly, it has been suggested that the immobilisation of Ca and P in the skeletons of large vertebrates can play an important role in terrestrial nutrient cycling (Coe, 1978).

Hyaenas have among the most powerful jaws and tooth strength of all large carnivores (Van Valkenburgh & Ruff, 1987). This allows them to break the bones of vertebrate prey species and access nutritious marrow and important phosphatic minerals, which are unavailable to most other vertebrate species (Skinner & Chimimba, 2005). Where bone scavengers are absent, skeletons may otherwise take 10-100s of years to decompose depending upon the environmental conditions (Carter et al., 2007; Coe, 1978). The creation of bone splinters by hyaenas at carcass sites has already been shown to provide an important source of Ca and P for griffon vultures. Where hyaenas were absent, osteodystrophy in vulture chicks due to Ca and P deficiency occurred in 17% of chicks, but no chicks suffered from this metabolic bone disease at sites where hyaenas were present (Richardson et al., 1986).

Here, we postulate that hyaenas may provide another mechanism of Ca and P recycling via the production of nutrient-enriched faeces. To date, studies examining terrestrial nutrient recycling in the faeces of large savannah vertebrates have primarily focused on herbivores (e.g. Doughty et al., 2016; Hempson et al., 2017; Veldhuis et al., 2018; Wolf et al., 2013). Due to their low population densities, nutrient recycling in the faeces of savannah carnivores has been considered negligible (Wolf et al., 2013). However, bones concentrate Ca and P approximately $10^4\times$ higher than in plant tissues (Brodie & McIntyre, 2019). This results in hyaena faeces that are considerably elevated in Ca and P (Kruuk, 1972). Furthermore, because hyaenas defecate in latrines—concentrated refuse areas for olfactory communication—the cycling of Ca and P in hyaena faeces may result in local sites of very high enrichment, which could influence soil properties, vegetation composition and tissue nutrient content (Janssens et al., 1998; Stevens et al., 2018).

Fresh hyaena faecal deposits are green-grey in colour (Figure 1a), but quickly turn white due to the presence of calcium phosphate within the faeces (Figure 1b; Larkin et al., 2000; Pesquero et al., 2013). In this inorganic white powder form (Figure 1c), hyaena faeces mimic the application of bone meal, a common fertiliser for soils, whereby stable Ca phosphates become increasingly soluble with decreasing soil pH (Jeng et al., 2007). In this way, the inorganic components of bone meal (faeces) act as slow-release mineral fertilisers (Brod et al., 2015). Much of sub-Saharan Africa has a soil pH < 7 (Hengl et al., 2015; Figure 2a), indicating that inorganic nutrients from hyaena faeces may form an important component of local biogeochemical cycles.

We tested the hypothesis that hyaenas play a role in recycling Ca and P within terrestrial landscapes by first comparing the

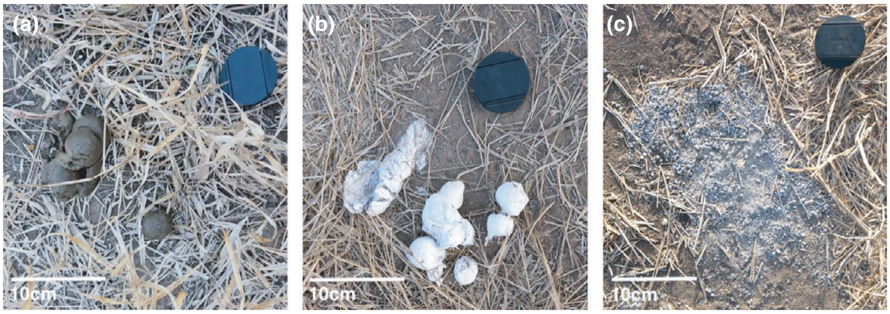

FIGURE 1 The breakdown of spotted hyaena (*Crocuta crocuta*) faeces from (a) brown-green fresh faeces (<12 h since defecation), to (b) white as it dries (days), and (c) after physical breakdown (weeks to months depending on environmental and biotic factors). Photos taken by A. Abraham in Manyeleti Nature Reserve (MNR) in July 2019

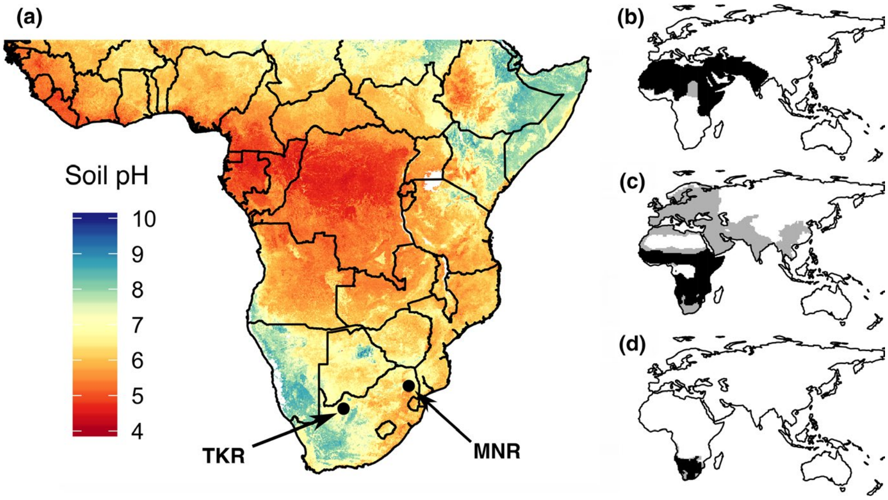

FIGURE 2 (a) Map of sub-Saharan Africa showing the location of Tswalu Kalahari Reserve (TKR) and Manyeleti Nature Reserve (MNR). Underlying map is surface soil (0-5cm) pH measured in H_2O from Hengl et al. (2015). Note: the inorganic fraction of hyaena faeces will only become bioavailable where soil pH < 7. Present (black) and present-natural (grey) species range for (b) *Hyaena* spp, (c) *Crocuta* spp and (d) *Parahyaena* spp adapted from PHYLACINE v1.2 (Faurby et al., 2018)

enrichment of Ca and P in hyaena faeces to other large savannah carnivores. For comparison, we quantified faecal concentrations from spotted hyaena (*Crocuta crocuta*) in the lowveld of South Africa and brown hyaena (*Parahyaenna brunnea*) in the southern Kalahari. We then compared the flux of minerals excreted in hyaena faeces from these sites to known important abiotic fluxes, including local weathering and atmospheric deposition rates.

2 | METHODS

2.1 | Study area

We calculated the flux of mineral recycling by spotted hyaena at Manyeleti Nature Reserve (MNR), a 23,750 ha wildlife reserve located at S 24°36′ and E 31°30′, which shares open boarders with the Kruger National Park and Associated Private Nature Reserves in the lowveld of South Africa (Figure 2a). MNR is situated on granitic substrate, which is poor in available P (~7 ppm) and Ca (~100 ppm), but mildly acidic (Hengl et al., 2017; Khomo, 2008; Steenkamp et al., 2018). Spotted hyaena density is estimated to be ~0.13 individuals km^{-2} (Mills et al., 2001). We calculated the flux of mineral recycling by brown hyaena at Tswalu Kalahari Reserve (TKR), a 121,700 ha wildlife reserve located at S 27°13′ and E 22°28′ in the southern Kalahari Desert, South Africa (Figure 2a). The substrate is primarily aeolian sands of the Gordonia formation, which is deficient in available P (~10 ppm) and less acidic than at MNR (Hengl et al., 2017; O'Halloran et al., 2010). The density of brown hyaena in the southern Kalahari has been estimated at ~0.018 individuals km^{-2} (Mills & Mills, 1982).

2.2 | Sample collection and analysis

For comparison, fresh (<12 h) faecal samples were collected opportunistically from six species of savannah carnivore: lion (*Panthera leo*), leopard (*Panthera pardus*), wild dog (*Lycaon pictus*), spotted hyaena (*Crocuta crocuta*), brown hyaena (*Parahyaenna brunnea*) and black-backed jackal (*Canis mesomelas*). Ten faecal samples were collected per species at each site, except for spotted and brown hyaena, which were collected only at MNR and TKR, respectively. Most samples were collected following observed defecation events. Additional samples were identified using spoor (Liebenberg, 1991) and scat characteristics (Estes, 1991). All samples were frozen within 5 h to −20°C and transported to the Endocrine Research Laboratory, University of Pretoria for lyophilisation at −54°C and ~0.96 mbar for 5–7 days until completely dry. Subsequently, dry faecal samples were pulverised by hand using a pestle and mortar and sifted through a plastic-mesh strainer to remove bone fragments. At the University of Pretoria Soil Sciences Laboratory, 0.25 g–0.30 g of dried faecal powder was digested in 10ml of Suprapur Nitric acid (65%) and analysed for P and Ca concentration using a SPECRO GENESIS Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES).

2.3 | Mineral recycling by hyaena

The flux of nutrients entering the ecosystem via the faeces of hyaena was calculated using equation 1:

$$\text{Faecal nutrient flux}(\text{g km}^{(-2)}\ \text{yr}^{(-1)}) = DM_f * C_f * D \qquad (1)$$

Where for each species, DM_f is the dry matter of faeces in g individual^{-1} year^{-1}, C_f is the mean faecal nutrient concentration in g g^{-1} from this study and D is the density of hyaena in individuals km^{-2} from literature sources outlined in Table 1. DM_f for each hyaena species was calculated using equation 2:

$$DM_f\left(\text{g ind}^{-1}\text{yr}^{-1}\right) = \frac{FMR}{E} * (1 - A) * T \qquad (2)$$

Where, FMR is the field metabolic rate calculated for an individual mammal in kJ day^{-1} by Nagy et al. (1999) based on body mass (BM) using the allometric relationship $4.82 * BM^{0.734}$. E is the metabolisable energy of a carnivore diet equivalent to 16.8 kJ g DM^{-1} from Nagy et al. (1999). A is the mean dry matter assimilation efficiency of 0.77 for carnivores from (De Cuyper et al., 2020) and T is 365 for the number of days in a year. The best estimate, lower and upper values for all parameters used in equations 1 and 2 are provided with references in Table 1 for each study site. Lower and upper estimates were calculated using minimum and maximum values from the literature for each parameter respectively (see Table 1). However, where only one value was given, we varied this by 10% to generate uncertainty bounds.

2.4 | Ethical statement

All samples were collected with the approval of the University of Pretoria Research and Animal Use and Care Committee (Reference EC043-18 and EC043-18-A1) and the South African Department of Agriculture, Forestry and Fisheries (DAFF-18/02/2019).

3 | RESULTS

Compared to other large savannah carnivores, brown and spotted hyaenas have higher concentrations of faecal Ca and P (Figure 3). Both hyaena species displayed overall average faecal concentrations of ~0.25 g Ca g^{-1} DM and ~0.12 g P g^{-1} DM, which is 4-30x greater than the mean of other carnivore species. The Ca and P concentration of non-hyaena species decreased with body size from lion (0.051 g Ca g^{-1} DM; 0.031 g P g^{-1} DM) to black-backed jackal (0.008 g Ca g^{-1} DM; 0.004 g P g^{-1} DM). For these species, there was no statistical difference in faecal nutrient concentration between

TABLE 1 Parameters used to calculate the best, lower and upper estimates of Ca and P recycling by spotted hyaena (*Crocuta crocuta*) at Manyeleti Nature Reserve (MNR) and by brown hyaena (*Parahyaenna brunnea*) at Tswalu Kalahari Reserve (TKR)

	Lower	Best estimate	Upper	Reference(s)
Spotted hyaena in lowveld (MNR)				
Body mass (kg)	54.5	65.4	75.5	Skinner and Chimimba (2005)
Field metabolic rate (kJ day^{-1})	14,439	16,507	18,342	Nagy et al. (1999)
Diet metabolisable energy (kJ g^{-1})	15.1	16.8	18.5	Nagy et al. (1999)
Assimilation efficiency (%)	0.69	0.77	0.85	De Cuyper et al. (2020)
Faecal matter (g DM_f day^{-1})	117	226	377	*This study*
Faecal Ca concentration (g g^{-1} DM_f)	0.186	0.250	0.314	*This study*
Faecal P concentration (g g^{-1} DM_f)	0.076	0.106	0.137	*This study*
Density (individuals km^{-2})	0.096	0.13	0.178	Mills et al. (2001)
Brown hyaena in southern Kalahari Desert (TKR)				
Body mass (kg)	35.7	38.9	42.1	Skinner and Chimimba (2005)
Field metabolic rate (kJ day^{-1})	10,585	11,273	11,947	Nagy et al. (1999)
Diet metabolisable energy (kJ g^{-1})	15.1	16.8	18.5	Nagy et al. (1999)
Assimilation efficiency (%)	0.69	0.77	0.85	De Cuyper et al. (2020)
Faecal matter (g DM_f day^{-1})	86	154	245	*This study*
Faecal Ca concentration (g g^{-1} DM_f)	0.205	0.249	0.292	*This study*
Faecal P concentration (g g^{-1} DM_f)	0.094	0.116	0.139	*This study*
Density (individuals km^{-2})	0.016	0.018	0.020	Mills and Mills (1982)

DM_f refers to dry matter of faeces.

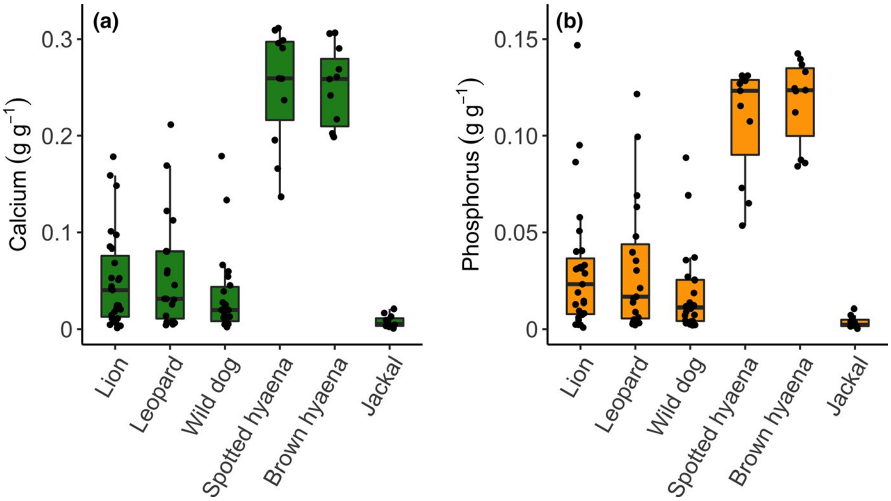

FIGURE 3 Faecal concentration measurements for six species of large carnivore for (a) calcium and (b) phosphorus. Individual points represent nutrient concentration from separate faecal samples

reserves. Lion, leopard and wild dog have high outlying points, indicating that non-hyaena species may occasionally pass bones through their digestive tract.

Spotted hyaenas were calculated to produce 226 [117–377] g faecal DM individual^{-1} day^{-1}, whilst brown hyaenas produced 154 [86–245] g faecal DM day^{-1} (Table 1). For spotted hyaena in MNR this translates into annual mineral recycling of 2681 [762–7691] g Ca km^{-2} year^{-1} and 1136 [312–3355] g P km^{-2} year^{-1}. However, for brown hyaenas in TKR, due to a significantly lower population density (see Table 1), mineral recycling was ~10× smaller at 253 [103–523] g Ca km^{-2} year^{-1} and 118 [47–249] g P km^{-2} year^{-1}.

4 | DISCUSSION

4.1 | Mineral fluxes

The concentration of Ca and P in hyaena faeces is between 1000–20,000× greater than local soil concentrations of these minerals at both MNR and TKR (Hengl et al., 2017). For spotted hyaena at MNR, this leads to a faecal deposition flux of P that is of a similar order of magnitude to other abiotic fluxes in the region. For example, Mahowald et al. (2008) estimate P deposition over the Kruger National Park between 100 and 500 g km^{-2} year^{-1}, which includes net deposition as a result of biomass burning. Additionally, Wolf et al. (2013) estimate a local rock weathering flux of P equal to 127.5 g km^{-2} year^{-1} based on rock mineral concentration and weathering rate. Together these abiotic fluxes, which constitute the primary input of P into MNR, provide an upper estimate of ~650 g P km^{-2} year^{-1}. This value is a little over half of that which we calculate annually being recycled in spotted hyaena faeces in MNR. Even in TKR, where the flux of P recycled within brown hyaena faeces is much smaller due to a lower population density (Table 1), the values are of the same order of magnitude to atmospheric deposition (Mahowald et al., 2008). However, given the less acidic nature of soils in the southern Kalahari (Figure 2a), minerals in faeces may take longer to become available to plants here. Absolute estimates of abiotic Ca fluxes in our study sites are lacking. However, Khomo (2008) finds that Ca is the most extensively leached element in southern parts of the Kruger National Park. Therefore, the importance of Ca contributions to soils via hyaena faeces is likely consistent with that of P in certain locations.

We also find that other large carnivores contribute to Ca and P recycling. However, this is variable, likely reflecting more sporadic ingestion of bones. Furthermore, hyaena preferentially break and consume larger animal bones (e.g. femurs), which are either inaccessible or often overlooked by other carnivores if alternative food sources are abundant (Valkenburgh & Ruff, 1987) thus highlighting the disproportionate role played by hyaena for re-mobilising nutrients stored in bones.

Hyaenas and other large carnivores are not adding ‘new’ minerals into the ecosystem, given that minerals from bones would eventually weather and be re-integrated into the soil. However, they do reduce the stock of immobilised minerals held in bones and vastly decrease the time for these minerals to become available. This process is akin to the role played by mammoths in mobilising nutrients locked up in vegetation across the northern high latitudes as suggested by Zimov et al. (1995). Further, due to their acidic digestive tract (Skinner & Chimimba, 2005), hyaena may also increase the partitioning of calcium phosphate to more soluble forms. Therefore, in sites where soil Ca or P occurs in low concentrations such as southern Kruger National Park (Khomo, 2008) or the southern Kalahari (Abraham et al., 2021), the re-mobilisation of nutrients by hyaenas from the bone to soil stock may play an important ecosystem role. If so, many ecosystems across Europe, Asia and parts of Africa, which lost hyaena genera during the late-Pleistocene extinctions (see Figure 2b–d) may have lost an important mechanism of nutrient fertilisation, and one for which other carnivores do not fully compensate.

4.2 | Latrines

Hyaena do not defecate evenly throughout the landscape, but in concentrated (1-800m^2) refuse areas called latrines (Skinner &

Chimimba, 2005). Latrines are used for months–years and can have between 2 and 60 individual stools present at any one time (Gorman & Mills, 1984; Vitale et al., 2020). Therefore, the geography of P and Ca input via the faeces of hyaena is strongly influenced by the geography of latrines, which are themselves a function of habitat, territorial boundaries and game drive roads (Hulsman et al., 2010; Vitale et al., 2020). Consequently, hyaenas potentially create nutrient hotspots within the landscape, which can influence many wider ecosystem processes including species diversity, decomposition rate and animal movement ecology. There are a number of beetle fauna that inhabit hyaena latrines (Krell et al., 2003), which may further redistribute minerals on the order of metres (Veldhuis et al., 2018; Vitale et al., 2020).

4.3 | Future research

At present, there are a number of outstanding questions, which prevent a comprehensive analysis of the role of hyaenas as agents of nutrient recycling. However, given the magnitude of the theoretical flux and the likely spatial aggregation of nutrients into latrines as presented in this paper, we believe this topic warrants further consideration. In particular, further research related to the physical and chemical composition of hyaena faeces, size and geography of latrines and effects of different environmental conditions on faecal leaching rates will assist in addressing current knowledge gaps.

ACKNOWLDEGEMENTS

The authors would like to thank Blaire Van Valkenburgh for insightful comments made during the preparation of this manuscript. Thanks are also extended to the Tswalu Foundation for financial assistance required to undertake this project and to Scott Abraham for field assistance.

CONFLICT OF INTEREST

All authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

AA, AW and JJ conceived the ideas and designed methodology; AA and AW collected the data; AA, TPJ and AW analysed the data; AA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data generated and analysed during this study is available via the Figshare repository: https://figshare.com/s/0e351eea70dd218f7ccf.

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How to cite this article: Abraham, A. J., Webster, A. B., Jordaan, J., Prys-Jones, T. O., Ganswindt, A., De Jager, P., & Doughty, C. E. (2021). Hyaenas play unique ecosystem role by recycling key nutrients in bones. *African Journal of Ecology*, 00, 1–6. https://doi.org/10.1111/aje.12907