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Consumption of hyaena faeces and artificial mineral licks by leopard tortoises (*Stigmochelys pardalis*) in a low-nutrient environment

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Abstract

Hyaena faeces and mineral licks represent highly concentrated nutrient resources for leopard tortoises (*Stigmochelys pardalis*) living in nutrient-poor environments. Here, we provide direct evidence for the consumption of hyaena faeces and artificial mineral licks by leopard tortoises in the Kalahari Desert. Tortoises aggregated at hyaena latrines and lick sites during the wet season between 10 AM and 6 PM in groups of 1–5 individuals. Where both salt and mineral licks were available, tortoises displayed a preference for salt. We suggest that calcium, phosphorus and sodium deficits are likely driving coprophagy and geophagy behaviours by tortoises in the Kalahari.

KEYWORDS
hyaena, Kalahari, mineral lick, nutrition, tortoise

Abstrait

Les excréments de hyène et les lèches minérales représentent des ressources nutritives très concentrées pour les tortues léopard (*Stigmochelys pardalis*) qui vivent dans des environnements pauvres en nutriments. Dans cette étude, nous fournissons des preuves directes de la consommation des excréments de hyène et de lèches minérales artificielles par les tortues léopards dans le désert du Kalahari. Les tortues se sont regroupées en groupes de 1 à 5 individus sur les excréments de hyène et les sites de léchage minérales pendant la saison humide, entre 10 heures et 18 heures. Lorsqu'il y avait à la fois du sel et des léchages de minéraux, les tortues montraient une préférence pour le sel. Notre hypothèse est que le manque de calcium, de phosphore et de sodium serait à l'origine des comportements de coprophagie et de géophagie chez les tortues dans le Kalahari.

1 | INTRODUCTION

Tortoises have a high-demand for calcium (Ca) and phosphorus (P) to grow their skeletons and protective carapace, while sodium (Na) is a key nutrient for metabolic, neural and muscular processes (Fledelius et al., 2005; Liesegang et al., 2007; Nagy & Medica, 1986). Most tortoises are exclusively or predominately herbivorous, including African genera (e.g. *Centrochelys*, *Stygmochelys*), but some

are omnivorous (e.g. *Kinixys*; Hailey et al., 1998; Luiselli, 2003). Consequently, vegetation is a primary source of Ca, P and Na for many tortoise species (Hazard et al., 2010). However, in some areas, nutrients available in vegetation do not satisfy total mineral requirements, causing tortoises to turn to alternative sources (e.g. geophagy, osteophagy; Moore & Dornburg, 2014; Sullivan & Cahill, 2019).

Wildlife concentrate nutrients into hotspots within the environment, which may become advantageous sites for tortoises to exploit. For example, some animals accumulate nutrients in communal defecation areas, called middens or latrines. A particularly striking occurrence of this is hyaena latrines, as the faeces of hyaenas are highly enriched with Ca and P from their diet of bones (Abraham et al., 2022). Similarly, wildlife managers also create nutrient hotspots in the form of artificial salt and mineral licks provided for large herbivores (Abraham et al., 2023). Such licks are, however, also frequented by nontarget species.

While the consumption of hyaena faeces and use of artificial mineral licks has often been discussed on tortoise nutrition forums, to the authors best knowledge, it is lacking formal observation in the wild. Here, we provide direct evidence of leopard tortoises (*Stigmochelys pardalis*) exploiting hyaena faeces and artificial mineral licks from a nutrient-poor environment in southern Africa.

2 | METHODS

2.1 | Study site

This study was conducted at the 120,000 ha Tswalu Kalahari Reserve (TKR), South Africa (S 27°13′30″, E 22°28′40″). Leopard tortoises are abundant throughout the Kalahari Desert (Baker et al., 2015) and commonly observed at TKR. Kalahari soils are generally considered nutrient-poor, with particularly low concentrations of P, Na and other important nutrients for tortoise health, such as zinc. This pattern is reflected in the availability of nutrients in vegetation at TKR (Figure 1; Abraham et al., 2023).

2.2 | Consumption of hyaena faeces

TKR has estimated densities of ~1.8/100 km^2 for brown hyaena and ~1.3/100 km^2 for spotted hyaena (Webster & Abraham, 2021). To understand how much hyaenas concentrate nutrients in their latrine sites, 10 faecal samples were collected from hyaena latrines in April–June 2019 and measured for Ca, P and Na concentration (for details, see Abraham et al., 2022). Eight Browning Recon Force Elite MP5 camera traps were placed at hyaena latrines during April 2024, set to record 30 s videos with 5-min intervals and left for ~20 days. We also opportunistically looked for the consumption of hyaena faeces by tortoises while in the field during this period. Such events were captured on video using an iPhone 8.

2.3 | Consumption of artificial mineral licks

Each year, ~10,000 kg of salt (Na) in ~60 kg blocks and ~25,000 kg of mineral lick (Ca, Cu, Co, Fe, I, Mg, Mn, Na, P, S, Se, Zn) in ~25 kg blocks are deployed across TKR by wildlife managers for resident large herbivores. Abraham et al. (2023) describes the concentrations of Ca, P and Na in these supplementary resources based on 20 samples for each of salt and mineral licks. Camera traps (same set up as above) were placed at 19 mineral lick sites in July–September 2021 and 12 sites in October–November 2022 and left for 7–30 days.

3 | RESULTS

3.1 | Tortoise consumption of hyaena faeces

From 3296 h of camera trap footage, we captured eight videos with at least one tortoise at a hyaena latrine site and four moments of direct faecal consumption. We also observed one tortoise approaching a hyaena latrine in-person. The tortoise examined available hyaena scat, found a bolus, but struggled to masticate and ingest

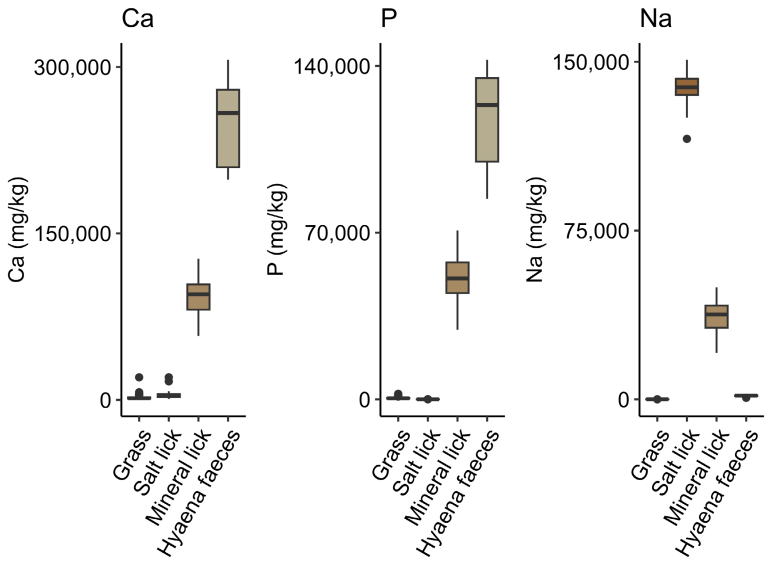

FIGURE 1 Comparison of nutrient (calcium [Ca], phosphorus [P] and sodium [Na]) concentrations across diet items of leopard tortoise (*Stigmochelys pardalis*) at Tswalu Kalahari Reserve (TKR). Compared with mean nutrient concentration in five common grasses at TKR: Hyaena faeces are ~130 times higher in Ca, ~210 times higher in P and ~10 times higher in Na; artificial mineral licks are ~50 times higher in Ca, ~90 times higher in P and ~225 times higher in Na; artificial salt licks are ~850 times higher in Na.

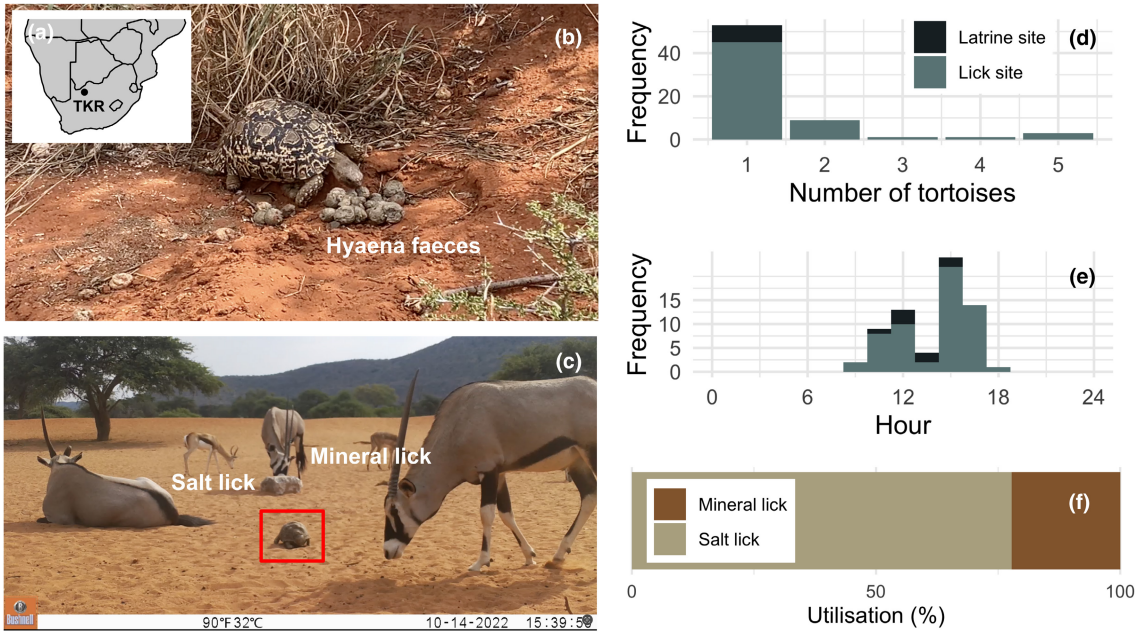

FIGURE 2 Characteristics of coprophagy and mineral lick use by leopard tortoises (*Stigmochelys pardalis*) at Tswlau Kalahari Reserve, South Africa, including (a) direct evidence for the consumption of (b) hyaena faeces, and (c) artificial salt and mineral licks; (d) most tortoises were observed alone, although groups up to five were seen; (e) tortoises generally frequented latrine and lick sites between 10 AM and 6 PM; (f) when both salt and mineral licks were available, tortoises displayed a preference for salt licks. A compilation video of leopard tortoises consuming hyaena faeces and artificial mineral licks is available at: https://www.youtube.com/watch?v=AxktyA1W6MQ.

it. The tortoise then used its front feet to break the bolus apart. Noticing a fresher scat, the tortoise abandoned the original scat and moved to break and consume the fresher scat. From our direct observation, we suggest that tortoises may be selectively searching for and ingesting bone fragments within hyaena scat.

3.2 | Tortoise consumption of mineral licks

From 7050 h of camera trap footage, we captured 59 videos with at least one tortoise at a lick site, four moments of direct mineral-lick use and 31 moments of salt-lick use. One site had five tortoises simultaneously utilising the same lick, highlighting that these are key sites of tortoise interaction (Figure 2d). We only observed tortoises during the warm-wet season (Oct–Nov), specifically at nine out of 12 mineral lick sites camera trapped during this period. Tortoises primarily utilised licks between 10 AM and 6 PM (Figure 2e). When both salt and mineral licks were in the camera frame, it appeared that salt was preferred over other minerals (Figure 2f).

4 | DISCUSSION

We observed leopard tortoises consuming both hyaena faeces and artificial mineral licks. However, it is likely that we underestimated the true occurrence, as tortoises are slow moving ectotherms and may not have always triggered our motion-sensor camera traps (Hobbs & Brehme, 2017). Hyaena faeces and artificial licks are enriched with 10–1000 times more Ca, P and Na than local grasses (Figure 1). Consuming these concentrated nutrient resources may help tortoises fulfil mineral requirements. However, we speculate that it may also influence dietary stoichiometry as the Ca:P ratio of hyaena faeces and mineral licks is ~2:1, but the optimal Ca:P ratio of tortoise diets is 3.1–5.8:1 (Hazard et al., 2010; Hetényi & Andrásofszky, 2022). Where nutrient intake or stoichiometric imbalances are excessive, tortoises may develop calcifications in their tissues or shell pyramiding (Fledelius et al., 2005; Liesegang et al., 2007). We observed pyramiding for some individuals at TKR, but further research is needed to examine the extent of this and if such effects are due to the consumption of hyaena faeces or artificial mineral licks.

While our findings do not provide ultimate evidence that leopard tortoise populations are Ca-, P- or Na- limited, they still hold important insights. Human activities are changing the spatial and temporal availability of concentrated nutritional resources. For example, the periodic removal of animals from TKR to prevent overgrazing leaches large quantities of Ca and P from the reserve in animal bones (Abraham et al., 2021), while some hyaena populations face an uncertain future due to pressures of human–wildlife conflict and face the threat of local declines or extirpations (Weise et al., 2015). Artificial licks may replace natural nutrient hotspots and are clearly being utilised by tortoises at TKR, but accessing these sites comes with additional dangers from other animals or potentially increased risk of disease transmission and human poaching (Wendland et al., 2010). For example, in one video, we observed that a juvenile tortoise was almost stepped on by a giraffe (*Giraffa camelopardalis*) while it consumed from a salt lick.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Select videos captured during fieldwork are available to watch at: https://www.youtube.com/watch?v=AxktyA1W6MQ.

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