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Anthropogenic supply of nutrients in a wildlife reserve may compromise conservation success

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ABSTRACT

In nutrient-poor wildlife reserves it has become common-practice to provide supplemental mineral resources for wildlife. Yet, the impacts of anthropogenic mineral supplementation on large herbivore nutrition, behaviour, and subsequent impact on ecosystem processes have received little attention. Here, we examine the contribution of anthropogenic mineral lick provision to wildlife nutrient intake across a community of mammalian herbivores (>10 kg) in the southern Kalahari Desert. Based on predicted daily nutrient intake and a faecal nutrient assessment, many large herbivore species appear deficient in phosphorus (P), sodium (Na), or zinc (Zn). For these nutrients, anthropogenic salt and mineral licks constitute an important source of nutrient intake helping to reduce or overcome requirement deficits. Larger-bodied species disproportionately consumed licks, acquiring more nutritional benefits. A comprehensive assessment of animal body condition indicated that, in general, large herbivores display good health. However, bulk grazers, non-ruminants and females displayed poorer body condition. We discuss how provisioning of anthropogenic mineral licks may inflate large herbivore populations beyond the long-term carrying capacity of the reserve by decoupling wildlife fecundity from nutrient-related feedbacks on population growth. Over time, this could compromise ecosystem integrity through habitat degradation, modified species interactions and trophic cascades. Based on results presented here, it is clear that anthropogenic provisioning of mineral licks should be considered cautiously by wildlife managers aiming to conserve natural processes in landscapes.

1. Introduction

The nutritional status of wildlife directly influences animal health, fertility, and susceptibility to disease and predation (Robbins, 2012; Milner et al., 2014). Consequently, human activities that limit access to or supplement nutrient resources can exert strong control over wildlife populations (Hobbs and Swift, 1985; Birnie-Gauvin et al., 2017; Abraham et al., 2023). For example, fences directly limit animal movement to high-resource areas (Pekor et al., 2019), while provisioning of supplementary nutrient resources in the form of ancillary feed, artificial mineral licks, bait, or carcasses can substantially augment local nutrient availability (Oro et al., 2013; Murray et al., 2016; Shutt and Lees, 2021).

The benefits of supplemental nutrition for animal health have been understood in livestock and hunting landscapes for thousands of years (Oro et al., 2013). In these settings, the aim is to maximise physical growth and population density of target species for increased harvest (McDowell, 1996; Bartoskewitz et al., 2003). Similar motives now exist in recreational landscapes, where increasing the health, density, and encounter rate of wildlife via mineral provisioning can lead to enhanced viewing experiences (Dubois and Fraser, 2013; Cox and Gaston, 2018). For example, to boost wildlife encounters, 64 % of households in the United Kingdom provide supplementary bird feed (Shutt and Lees, 2021), with an average of 100 bird feeders per km^2 (Cox and Gaston,

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2018).

While the impact of supplementary feeding on wildlife nutrition, behaviour and subsequent influence on ecosystem processes (e.g., interspecific competition) has been explored for some taxa (e.g., birds; Shutt and Lees, 2021), little attention has been directed towards large mammalian wildlife (Brown and Cooper, 2006; Milner et al., 2014), despite its common practice worldwide (e.g., Felton et al., 2017; Simpson et al., 2020; Abraham et al., 2021). Indeed, supplementary feeding of large mammals has mostly retained a production-oriented approach inherited from its agricultural origins. In conservation areas, this may become problematic if excessive provision inflates herbivore population densities above the long-term carrying capacity of the ecosystem. In the absence of disease or predation, large herbivore population density stabilises at the ecosystem carrying capacity, which is limited by the availability of water, energy, and nutrients (Chapman and Byron, 2018). As herbivore density increases, so does intra- and inter-species competition for resources, which leads to lower body condition and recruitment rates (Van der Waal et al., 2003; Lane et al., 2014). As a result, anthropogenic nutrient resources may decouple wildlife fecundity from nutrient-related feedbacks on population growth (Milner et al., 2014).

Inflated wildlife densities could compromise the integrity and stability of ecosystems due to issues of (i) habitat degradation through overgrazing and soil compaction (Felton et al., 2017; Abraham et al., 2021), (ii) altered inter- and intra-species competition due to changes in animal movement patterns and competitive advantages (Van der Waal et al., 2003; Milner et al., 2014), and (iii) trophic cascades as a result of modified trophic webs, such as increased predator abundance (Oro et al., 2013). Accordingly, if anthropogenic nutrient resources are provided in conservation areas, it is important to ascertain which species consume the licks, to what extent licks contribute to nutrient intake, and how provision of licks may impact broader ecosystem processes.

In this study, we examine the relative contribution of anthropogenic mineral lick provision to nutrient intake across a large (>10 kg) mammal community in the southern Kalahari Desert. Given this region is nutrient-poor (Cromhout, 2007), mineral licks may contribute substantially to nutrient intake by large herbivores (Knight et al., 1988). We assessed how provisioned nutrients may influence wildlife health using two commonly employed metrics: (i) an assessment of faecal nutrient concentrations, and (ii) an assessment of animal body condition. Finally, we discuss the role that anthropogenic mineral provision may have on broader ecosystem dynamics and for achieving conservation goals.

2. Methods

2.1. Study site

Tswalu Kalahari Reserve (TKR) is a 110,880 ha fenced wildlife reserve centred at −27.26, 22.45 in the southern Kalahari Desert, South Africa (Fig. 1a). Prior to 1995, TKR comprised ~40 domestic livestock farms, but was converted to a wildlife reserve by the removal of internal fences and associated infrastructure. The foundational principle of TKR is ecological restoration financed by tourism (https://tswalu.com/conservation-story/conservation/). Today, TKR includes a complement of large vertebrate herbivores native to the region, as well as a number of species that would historically have occurred seasonally but are now resident within the fenced system (see Table 1; van Rooyen and van Rooyen, 2022). An electrified fence divides the reserve into two sections; the Greater Korannaberg section (92,231 ha), which harbours cheetah (*Acinonyx jubatus;* 4.3 ind.100 km^{-2}), African wild dog (*Lycaon pictus*; 0.4 ind.100 km^{-2}) and spotted hyaena (*Crocuta crocuta*; 1.3 ind.100 km^{-2}), and the Lekgaba section (18,649 ha), which supports two prides of lion (*Panthera leo*; 5.9 ind.100 km^{-2}) (Fig. 1).

Much of TKR is underlain by aeolian sands of the Gordonia formation, with the emerging Korannaberg mountains formed of subgraywacke, quartzite, slate, dolomite, jasper and conglomerate (van Rooyen and van Rooyen, 2022). Sands of the southern Kalahari contain low concentrations of many critical nutrients for animal health, including nitrogen (N), phosphorus (P), sodium (Na), copper (Cu) and zinc (Zn) (Knight et al., 1988; Grant et al., 1996; Cromhout, 2007). As a result, TKR managers provide supplementary nutrients in the form of anthropogenic ~62 kg salt (Na) and ~ 25 kg mineral (Ca, Cu, Co, Fe, I, Mg, Mn, Na, P, S, Se, Zn) licks, distributed throughout the reserve (Fig. 1b-g; Abraham et al., 2021). These licks are purchased from local suppliers (https://safarifeeds.co.za/products) and placed near water sources throughout TKR (Greater Korannaberg 15 sites, Lekgaba 7 sites; see Fig. 1a). Licks are replenished within days of being consumed, ensuring constant availability throughout the year. In total, TKR provides 8–10,000 kg salt and 20–25,000 kg mineral lick per year across the reserve. Information pertaining to lick provision for the Greater Korannaberg and Lekgaba sections separately is not available. Consequently, both sections are considered together.

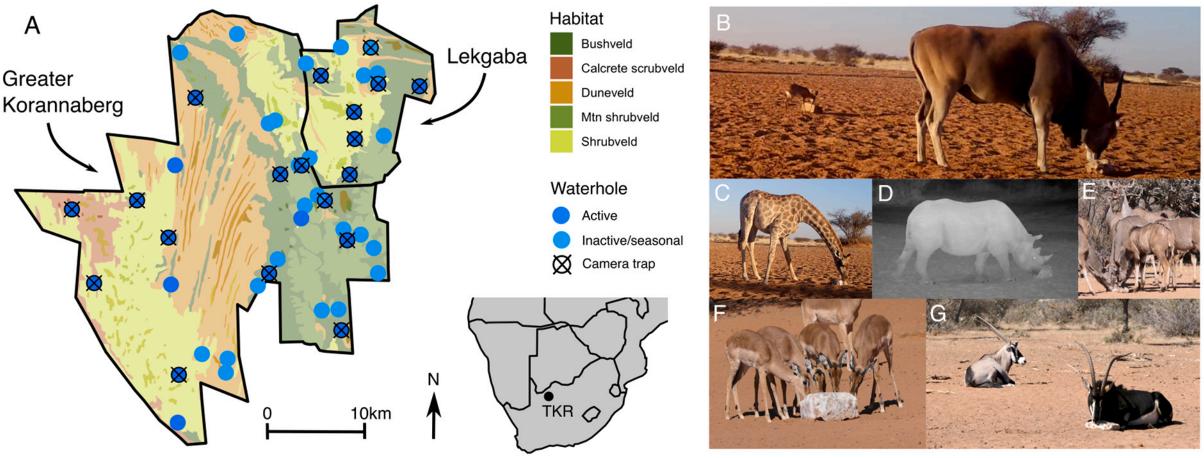

Fig. 1. (A) Tswalu Kalahari Reserve (TKR), South Africa, highlighting the Greater Korannaberg and Lekgaba sections, major habitat types (van Rooyen and van Rooyen, 2022) and the location of waterholes. Sites where camera traps were placed at salt and mineral licks to observe utilisation by large herbivores (>10 kg) are denoted. Salt and mineral lick consumption by (B) steenbok (*Raphicerus campestris*) and eland (*Taurotragus oryx*), (C) giraffe (*Giraffa camelopardalis*), (D) black rhino (*Diceros bicornis*), (E) kudu (*Tragelaphus strepsiceros*), (F) impala (*Aepyceros melampus*), and (G) gemsbok (*Oryx gazella*) and sable (*Hippotragus niger*) at TKR. Photos taken by A. Abraham and A. Webster.

Table 1

Characteristics and nutrient requirements for maintenance in ungulates resident at Tswalu Kalahari Reserve. Body mass and digestive physiology values taken from Hempson et al. (2015), dietary C_4% from [a]Codron et al. (2006), [b]Codron et al. (2007), [c]Strauss (2015) and [d]Staver and Hempson (2020) and nutrient requirements from Lintzenich and Ward (1997).

Species	Mass (kg)	Digestive physiology	C_4% in diet	Intake requirement (mg.day^{-1})							
				Ca	Cu	Fe	Mg	Mn	Na	P	Zn
White rhino (*Ceratotherium simum*)	2196	Non-ruminant	90.0 [d]	43,530	195	784	15,240	784	16,930	32,650	784
Giraffe (*Giraffa camelopardalis*)	1118	Ruminant	5.0 [d]	17,290	69	311	10,380	208	6400	11,530	173
Black rhino (*Diceros bicornis*)	1000	Non-ruminant	9.0 [b]	24,440	110	440	8500	440	12,200	18,330	440
Eland (*Taurotragus oryx*)	511	Ruminant	11.8 [d]	9740	39	175	5840	117	3610	6490	97
Buffalo (*Syncerus caffer*)	486	Ruminant	94.0 [d]	9390	38	169	5630	113	3480	6260	94
Plains zebra (*Equus quagga*)	280	Non-ruminant	92.0 [d]	9610	43	173	3360	173	3740	7210	173
Mountain zebra (*Equus zebra*)	279	Non-ruminant	90.0 [c]	9560	43	172	3350	172	3720	7170	172
Roan (*Hippotragus equinus*)	264	Ruminant	96.8 [d]	6000	24	108	3600	72	2200	4000	60
Blue wildebeest (*Connochaetes taurinus*)	220	Ruminant	95.0 [d]	5250	21	94	3150	63	1940	3500	52
Sable (*Hippotragus niger*)	211	Ruminant	96.5 [d]	5080	20	91	3050	61	1880	3390	51
Gemsbok (*Oryx gazelle*)	204	Ruminant	85.7 [d]	4960	20	89	2970	59	1840	3300	50
Kudu (*Tragelaphus strepsiceros*)	202	Ruminant	4.8 [d]	4930	20	89	2960	59	1830	3290	49
Red hartebeest (*Alcelaphus buselaphus*)	150	Ruminant	99.3 [d]	3970	16	71	2380	48	2380	2640	40
Warthog (*Phacochoerus africanus*)	76	Non-ruminant	91.0 [b]	3680	17	66	1290	66	1290	2760	66
Impala (*Aepyceros melampus*)	49	Ruminant	54.3 [d]	1740	7	31	1050	21	1050	1160	17
Springbok (*Antidorcas marsupialis*)	35	Ruminant	23.0 [d]	1370	5	25	820	16	820	910	14
Baboon (*Papio ursinus*)	30	Non-ruminant	30 [a]	1860	8	34	650	34	650	1400	34
Common duiker (*Sylvicapra grimmia*)	17	Ruminant	7.5 [d]	800	3	14	480	10	480	530	8
Steenbok (*Raphicerus campestris*)	11	Ruminant	13.3 [d]	590	2	11 1	350	7	350	390	6

Note, nutrient intake requirements do not represent determined minimum thresholds below which animal health is immediately compromised, but instead are descriptions from zoo nutritionists that contain an unknown safety margin.

2.2. *Large herbivore abundance*

At TKR, large herbivore (>10 kg) aerial counts are conducted annually during the beginning of the dry season (March–April). We transformed raw count data for each species into an estimate of abundance using the principles of 'distance' sampling (see Text S1 for details and comparison to ground-based validation; Buckland et al., 2015). Large herbivore abundance estimates for the Greater Korannaberg and Lekgaba sections are provided in Table S1.

2.3. *Large herbivore nutrient intake*

In natural environments, large mammalian herbivores primarily acquire nutrients from forage and water (Robbins, 2012). Our aim here is to contextualize nutrient acquisition from anthropogenic mineral licks at TKR compared to other major sources. Whilst geophagy (ingestion of soil) and osteophagy (ingestion of bone) are known contributors of nutrition for Kalahari herbivores, from steenbok (*Raphicerus campestris*) to elephant (*Loxodonta africana*) (Knight et al., 1988; Holdø et al., 2002), we do not currently have estimates for these sources.

2.3.1. *Natural forage intake*

Plant nutrient content notably varies between grasses and woody plants, and by season (Kattge et al., 2020). To account for differences in herbivore diet, we obtained the contribution of C_4 plants (i.e., grasses) to the diet of each species (see Table 1; Codron et al., 2007; Staver and Hempson, 2020). We then collated leaf nutrient concentration data from previous studies at TKR and our own extensive field campaign (see Text S2 for details). Due to inconsistencies between study methodologies (e.g., plant species collected, nutrients measured), we could not reliably assess forage nutrient phenology, but instead calculated a mean annual nutrient concentration for C_3 and C_4 plant groups (Table S2). Daily forage nutrient intake for an individual of each species was calculated using Eqs. (1) and (2):

$$NI_{C3_{i,j}} = C_{C3_i} * DMI_j * \left(1 - \%C4_j\right) \tag{1}$$

$$NI_{C4_{i,j}} = C_{C4_i} * DMI_j * \%C4_j \tag{2}$$

where $NI_{C3,i,j}$ and $NI_{C4,i,j}$ is the nutrient intake from C_3 and C_4 plants of nutrient *i* for an individual of species *j* in mg.day^{-1}, $C_{C3,i}$ and $C_{C4,i}$ are the average concentrations of nutrient *i* in mg.g dry matter^{-1} of C_3 and C_4 plants, DMI_j is dry matter intake estimated using the allometric relationship for field metabolic rate of $4.82*BM^{0.734}$ and metabolizable energy of the diet for species *j* equal to 10 kJ.g DM^{-1} for hindgut fermenters and 11.5 kJ.g DM^{-1} for ruminants from Nagy et al. (1999), and $\%C4_j$ is the percentage of C_4 plants in the diet of species *j*.

2.3.2. *Water*

Water quality surveys have been conducted extensively at TKR over the period 2000–2021 (see Text S3 for details). Here, we calculated the mean nutrient concentration from all waterholes sampled across TKR. Daily water nutrient intake for an individual of each species was estimated using the allometric relationship of daily water requirements from Calder and Braun (1983):

$$NI_{water_{i,j}} = C_{water_i} * 99 * BM_j^{0.9} \tag{3}$$

where $NI_{water,i,j}$ is the nutrient intake from water of nutrient *i* for an individual of species *j* in mg.day^{-1}, $C_{water,i}$ is the concentration of nutrient *i* in water in mg.litre^{-1}, and BM_j is the body mass in kg for an individual of species *j*.

2.3.3. *Salt and mineral licks*

Both salt and mineral licks, placed near waterholes in a 1:1 ratio, are used at TKR. Notably, mineral licks also contain Na, albeit at a lower concentration than salt licks (for their mineral composition, see Table S2). To quantify salt and mineral lick consumption by large herbivore species, Bushnell TrophyCam HD and Browning Recon Force ADVANTAGE camera traps were placed at lick sites between July–September 2021. Camera traps were programmed to record 30s videos with a 5-minute interval between recordings and left for 14 days. We recorded all large herbivore species (>10 kg) present within the camera trap frame and the number of animals that utilised salt and mineral licks respectively. To ensure each camera trap contributed equally to data analysis, visitation rate from each camera trap was standardised /24 h. We assume that 75 % of licks are consumed by large herbivores, with the rest being consumed by other fauna (e.g., birds) or lost to the environment. We cannot measure how much lick is consumed during each discrete feeding event, but we do know the total quantity consumed in

TKR annually (~9000 kg salt lick; ~22,500 kg mineral lick). We therefore divide the total lick consumption over the course of a year by the abundance and proportional use of licks by each species, with the assumption that an individual consumes proportionally to their metabolic rate (i.e., $BM^{0.75}$) during each feeding event (Shipley et al., 1994). We calculated individual daily nutrient intake from salt and mineral lick consumption using Eqs. (4) and (5):

$$NI_{salt\_lick_{i,j}} = C_{salt\_lick_i} * M_{saltlick} * F * \frac{BM_j^{0.75} * CT_{salt\_lick_j}}{\sum_{j=1}^{j} BM_j^{0.75}} * \frac{1}{A_j * 365} \quad (4)$$

$$NI_{mineral\_lick_{i,j}} = C_{mineral\_lick_i} * M_{mineral\_lick} * F * \frac{BM_j^{0.75} * CT_{mineral\_lick_j}}{\sum_{j=1}^{j} BM_j^{0.75}} * \frac{1}{A_j * 365} \quad (5)$$

where $NI_{salt\ lick,i,j}$ and $NI_{mineral\ lick,i,j}$ are the nutrient intake of nutrient *i* from salt lick and mineral licks respectively for an individual of species *j* in $mg.day^{-1}$, $C_{salt\ lick,i,j}$ and $C_{mineral\ lick,i,j}$ are the concentrations of nutrient *i* in salt and mineral licks in $mg.g^{-1}$ (Table S2), $M_{salt\ lick}$ and $M_{mineral\ lick}$ are the mass of licks distributed within TKR in $g.year^{-1}$, F is the fraction of available lick consumed by large herbivores (>10 kg) set to 0.75 (see above), BM_j is the body mass of species *j* (Table 1), $CT_{salt\ lick,j}$ and $CT_{mineral\ lick,j}$ are the use of salt and mineral licks by species *j* as a proportion of all species determined by camera traps and A_j is the abundance of species *j* as determined by aerial counts, calculated as described in Section 2.2 and supplementary text S1.

2.4. Large herbivore nutrient requirements

To contextualize total nutrient intake, including estimates of nutrient intake from mineral licks, we compared total nutrient consumption to estimates of nutritional requirements of each species. We compared our average estimates of nutrient intake from forage, water, and mineral licks to suggested requirements from Lintzenich and Ward (1997) for adult zoo animals at maintenance. This allows us to contextualize the contribution of anthropogenic mineral licks, but we recognise that our approach overlooks critical seasonal (e.g., climatic) and individual (e.g., age, sex) differences (Tait and Fisher, 1996; Robbins, 2012; Suttle, 2010). We specifically focus on calcium (Ca), phosphorus (P), sodium (Na), zinc (Zn), copper (Cu), iron (Fe), magnesium (Mg) and manganese (Mn), which are all nutrients closely linked to health and reproduction in large mammals (Robbins, 2012; Suttle, 2010). Species-specific nutrient requirements were calculated using Eq. (6):

$$NI_{requirement_{i,j}} = \frac{RC_{i,j}}{0.9} * DMI_j \quad (6)$$

where $NI_{requirement,i,j}$ is the required intake of nutrient *i* for species *j* in $mg.day^{-1}$, $RC_{i,j}$ is the required concentration of nutrient *i* for adult maintenance in mg.g dry $matter^{-1}$ on a 90 % dry matter basis for species *j* defined by Lintzenich and Ward (1997), and DMI_j is estimated as in Eqs. (1) and (2). Table 1 outlines species-specific mass, digestive physiology and daily nutrient intake requirements.

2.5. Index of large herbivore nutrient stress

Acquiring direct measurements on the nutrient status of large wild herbivores is difficult without substantial and costly interference to the animals (Robbins, 2012; Birnie-Gauvin et al., 2017). Faecal nutrient analysis, however, offers a practical, non-invasive approach to measure nutrient stress and has been extensively applied to large herbivores, including buffalo, zebra, giraffe, roan, kudu, springbok and elephant (e.g. Wrench et al., 1997; Grant et al., 2000; Van der Waal et al., 2003; Stapelberg et al., 2008; Okita-Ouma et al., 2021). Faecal measurements reflect the quality and digestibility of resources consumed by an individual and can be used to assess if the animal's diet contains enough energy and protein to utilise additional nutrients acquired from mineral licks (McDowell, 1996; Steuer et al., 2014). If energy or protein are insufficient, the provision of additional nutrients serves no purpose and can even have negative effects for animal health by creating harmful free radicals leading to oxidative stress (Van Niekerk and Jacobs, 1985; Goff, 2018).

We collected fresh faeces (<10 min post-defecation) from three abundant ruminant species representing three feeding types; blue wildebeest (*Connochaetes taurinus*; grazer), springbok (*Antidorcas marsupialis*; mixed feeder) and kudu (*Tragelaphus strepsiceros*; browser). Faecal collection (60 per species; total $n = 180$) was conducted coincident with camera trapping (July–September i.e., the dry season), when herbivores in the southern Kalahari are typically nutritionally stressed (Abraham et al., 2021). All faecal samples were lyophilised and homogenised prior to quantification of crude protein content, expressed as N, using a LECO® instrument equipped with TruMac CN/N determinator software (v1.5×) for instrument control and data processing. We then used Suprapur Nitric acid (65 %) digestion and SPECRO GENESIS Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES) quantification to determine P concentration in the same herbivore faecal samples. We compared faecal macro-nutrient (N and P) concentrations to thresholds of potential concern (cut-off values below which mammalian herbivores have been documented suffering from growth and reproductive issues). Similar thresholds of potential concern have not been established for micro-nutrients and thus we focus our faecal analysis on N and P only. For N we used 14 $g.kg^{-1}$ (grazers; Wrench et al., 1997) and 15 $g.kg^{-1}$ (mixed feeders and browsers; Van der Waal et al., 2003) and for P we used 2 $g.kg^{-1}$ (all species; Wrench et al., 1997). Different N thresholds were used for grazers and browsers due to the precipitating effect of condensed tannins elevating faecal N concentrations (Leslie et al., 2008; Steuer et al., 2014).

2.6. Large herbivore body condition

Nutritional intake has been directly linked to visual body condition in southern African herbivores (Grant et al., 2000; Van der Waal et al., 2003; Lane et al., 2014). We therefore undertook a comprehensive assessment of large herbivore body condition using a visual assessment scheme that relies on objective assessment of clearly detectable characteristics (such as the protrusion of ribs vs the presence of fat deposits; see Text S4 and Table S2 for methodological details; Ezenwa et al., 2009). Body condition score (BCS; 1 low to 5 high), species and sex were recorded for all individuals encountered along 1009 km of driven road transects conducted coincident with the camera trap survey and faecal collection. If large herbivores are nutritionally compromised at TKR, low body condition scores would be expected.

2.7. Statistical comparison between species and functional groups

All statistical analyses were conducted in R version 3.6.1 (R Core Team, 2019). We used ordinary least squares (OLS) regression to compare relative use of lick site, salt licks and mineral licks to species body mass. To satisfy assumptions of data normality, body mass and relative lick use were $\log_{10}$-transformed. Wilcoxon rank sum tests were used to compare differences between functional groups (e.g., diet, digestive physiology, sex) for percentage of nutrient intake compared to requirements and animal body condition. A one-way analysis of variance (ANOVA) with a post-hoc Tukey's test was used to statistically compare differences in faecal nutrient concentrations across species.

3. Results

3.1. Contribution of anthropogenic mineral licks to herbivore nutrient requirements

From camera traps deployed at 19 anthropogenic mineral lick sites, we recorded 38,984 large vertebrate animal sightings. Specifically, 12,764 animals were recorded directly using salt licks and 5722 utilising mineral licks. After accounting for abundance, results from ordinary least squares models indicate that lick site visitation ($t(17) = 3.73$, $p < 0.002$), salt lick use ($t(17) = 4.29$, $p < 0.001$), and mineral lick use ($t(17) = 3.79$, $p < 0.002$) all scaled positively with body mass (Fig. 2). Mean daily individual salt lick consumption varies from 0.004 g.day^{-1} (steenbok) to 11.9 g.day^{-1} (black rhino; *Diceros bicornis*), whilst mineral lick consumption varies from 0.04 g.day^{-1} (steenbok) to 48.5 g.day^{-1} (white rhino; *Ceratotherium simum*).

Based on our estimates of total nutrient intake, several large herbivore species at TKR consumed Cu, Na, P and Zn in amounts lower than required (Fig. 3), but all were replete in Ca, Fe, Mg and Mn (Fig. S3). Wilcoxon rank sum tests indicated that grazers were statistically more deficient in P than browsers ($W = 86$, $p < 0.001$), and hindgut fermenters more deficient in Cu ($W = 0$, $p < 0.001$), Na ($W = 13$, $p < 0.05$), P ($W = 4$, $p < 0.001$) and Zn ($W = 0$, $p < 0.001$) compared to ruminants. Salt and mineral licks constituted a substantial (>10 %) component of daily intake of Na for most large herbivore species, and > 45 % for black rhino, eland (*Taurotragus oryx*) and buffalo (*Syncerus caffer*). Many species acquire >10 % of daily P intake from mineral licks, with plains zebra (*Equus quagga*) the most at 19 %.

3.2. Assessment of large herbivore health

A one-way ANOVA with a post-hoc Tukey's test indicated that faecal N concentration statistically increased from blue wildebeest to kudu to springbok ($F(2,177) = 305.8$, $p < 0.001$). Faecal P concentration was also higher in springbok than blue wildebeest and kudu ($F(2,177) = 21.4$, $p < 0.001$). 92 % of kudu (browsers) and 100 % of springbok (mixed feeders) faecal samples were above the N threshold of potential concern, suggesting that most individuals from these groups may have had sufficient protein in their diet to utilise provisional nutrients acquired from anthropogenic salt and mineral licks (Fig. 4). However, 82 % of blue wildebeest (grazer) faecal samples were below the critical N threshold of potential concern. Mean faecal P concentration was below the threshold of potential concern for blue wildebeest and kudu, whilst 43 % of springbok samples were below the threshold of potential concern.

In total, 1865 BCS were obtained from TKR. Generally, large herbivores (>10 kg) are in reasonable health with a mean BCS of 2.97. Wilcoxon rank sum tests indicated that grazers display statistically lower body condition than browsers ($W = 299{,}031$, $p < 0.001$; Fig. 5a), hindgut fermenters display lower body condition that ruminants ($W = 171{,}140$, $p < 0.001$; Fig. 5b), and females display lower body condition than males ($W = 221{,}974$, $p < 0.001$; Fig. 5c).

4. Discussion

4.1. Mineral licks as an important source of nutrients

Many large herbivores at TKR appear deficient in Na, P and Zn. For these nutrients, anthropogenic salt and mineral licks constitute an important source of intake, helping to reduce or overcome nutrient deficits for many species (Fig. 3). This is especially true for larger-bodied species that consume licks disproportionately more (Fig. 2). Values of anthropogenic lick consumption calculated in this study compare similarly to other non-pastoral systems (e.g. ~18 g.day^{-1} by white-tailed

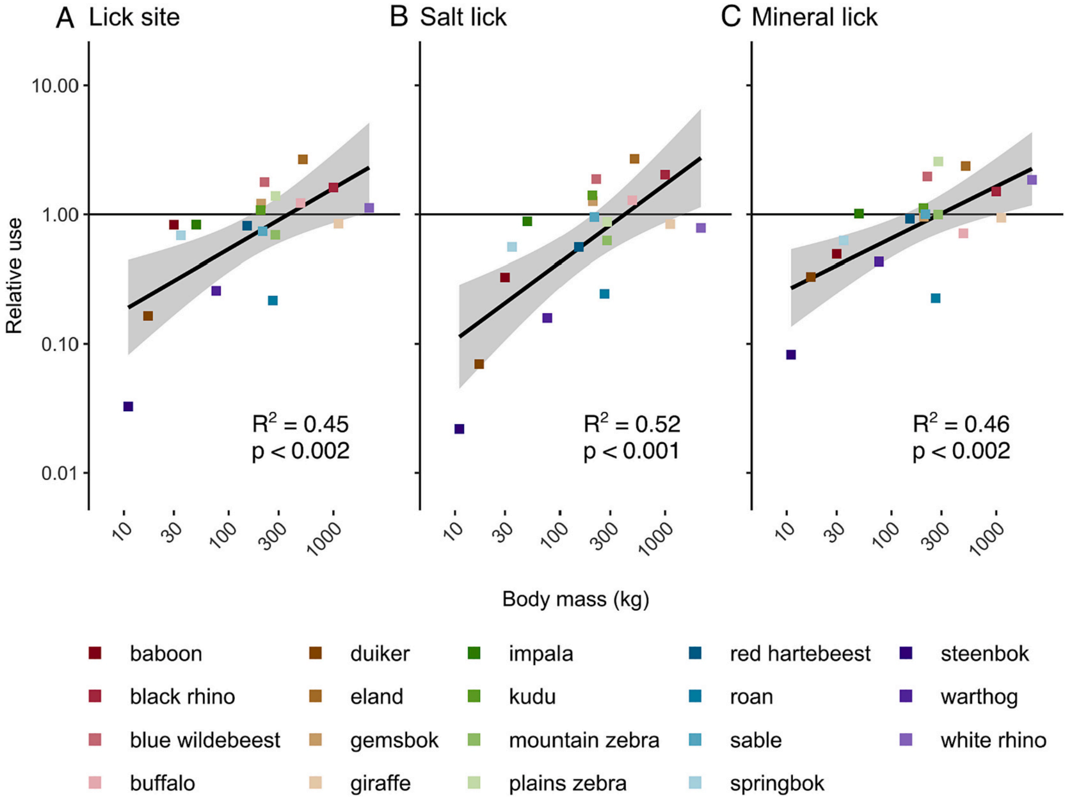

Fig. 2. Relative visitation of large herbivores to anthropogenic lick sites (A), and direct use of salt (B) and mineral (C) licks compared to body mass at Tswalu Kalahari Reserve (TKR). Note that the y-axis is scaled log$_{10}$, where values >1 represent more visitations of licks than expected based on species abundance and values <1 represent fewer visitations that expected. Trendlines represent ordinary least squares (OLS) model fit for all herbivores.

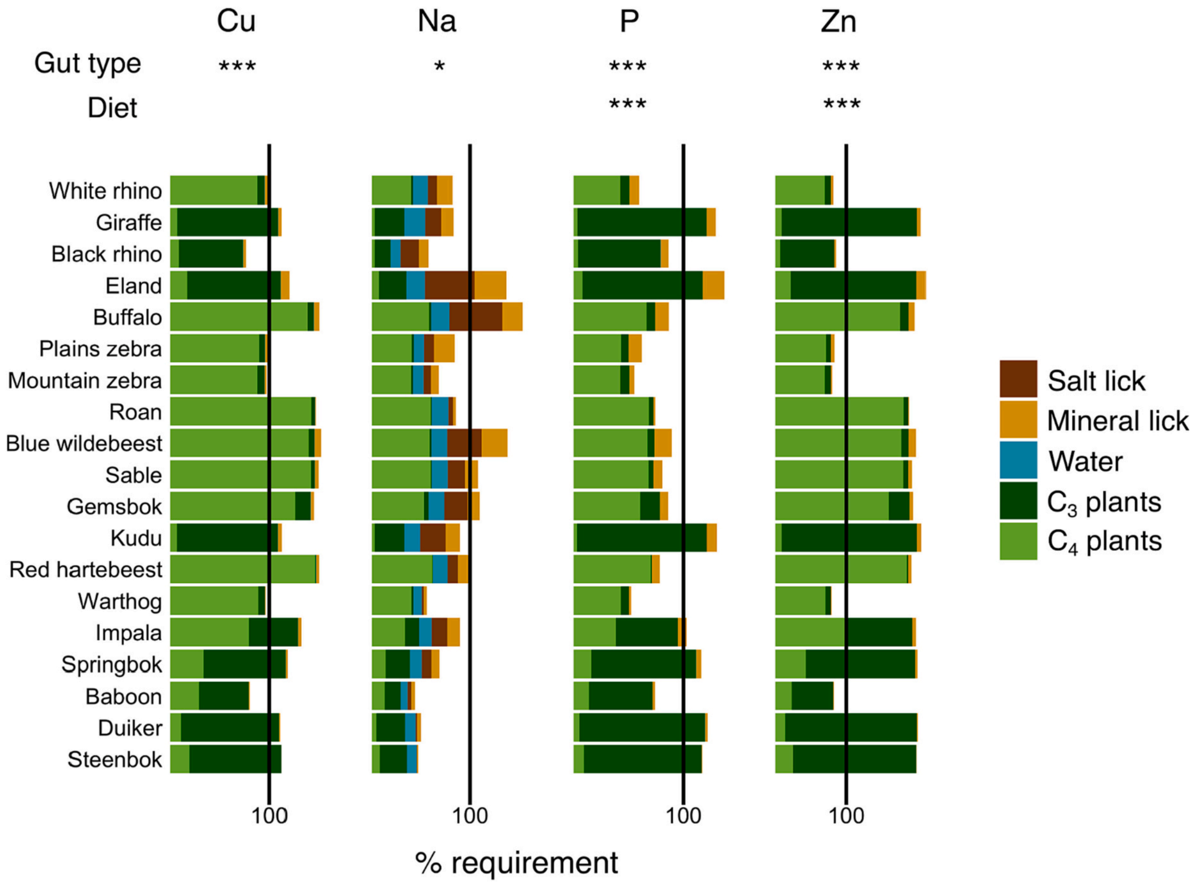

Fig. 3. Daily intake of copper (Cu), sodium (Na), phosphorus (P) and zinc (Zn) from different nutrient pools by large herbivores (>10 kg) at Tswalu Kalahari Reserve (TKR). Vertical lines represent optimal daily nutrient requirements for adult individuals at maintenance as suggested by Lintzenich and Ward (1997). Significant differences determined by Wilcoxon rank sum tests between gut type (ruminant vs non-ruminant) and diet (grazer vs browser) are denoted, where $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***). Species digestive physiology and diet traits are described in Table 1.

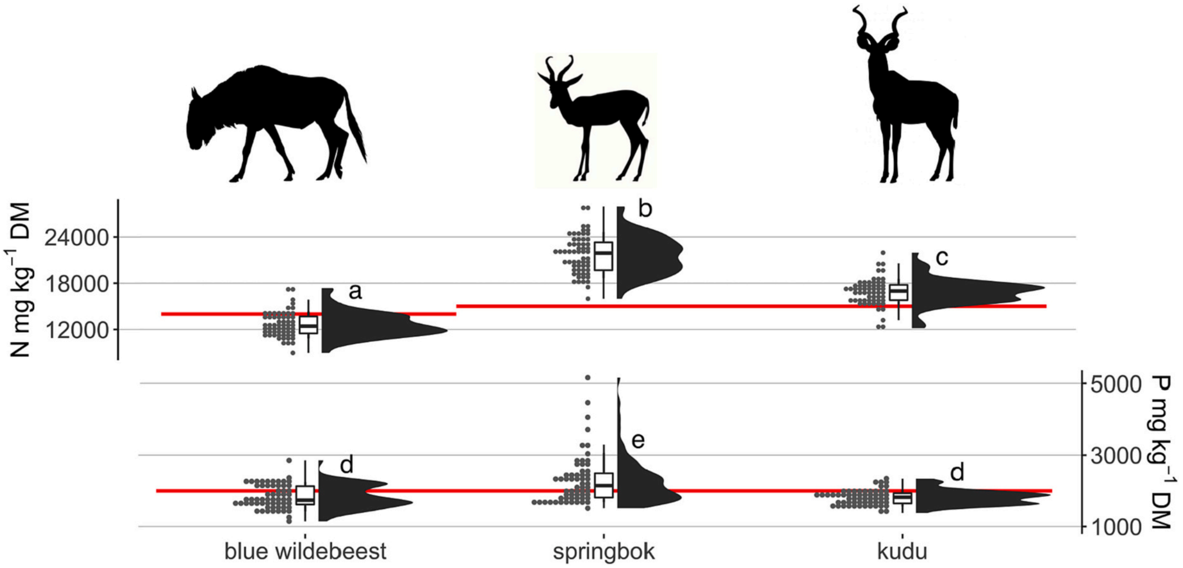

Fig. 4. Faecal macro-nutrient concentrations of nitrogen (N) and phosphorus (P) for blue wildebeest (*Connochaetes taurinus*; grazer), springbok (*Antidorcas marsupialis*; mixed feeder) and kudu (*Tragelaphus strepsiceros*; browser) resident at Tswalu Kalahari Reserve (TKR). Letters signify statistically significant ($p < 0.001$) differences between groups from an analysis of variance (ANOVA) with a post-hoc Tukey's test. Red lines represent minimum faecal nutrient thresholds below which large mammalian herbivores begin suffering growth and reproductive issues. The N threshold is 14,000 mg kg^{-1} for grazers and 15,000 mg kg^{-1} for mixed feeders and browsers. The P threshold is 2000 mg kg^{-1} for all species. Note that faeces were collected in the dry season (July–September) when nutrient stress is typically greatest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

deer (*Odocoileus virginianus*) in Louisiana, USA; Schultz and Johnson, 1992), suggesting that provisioning of supplementary nutrient resources may be similarly important for large herbivore communities in other nutrient-poor systems.

It is important to note that the data used to estimate nutrient requirements for this study (i.e. Lintzenich and Ward, 1997) do not represent determined minimum thresholds below which animal health is immediately compromised. Instead, they are descriptions from zoo nutritionists that contain an unknown safety margin, below which an individual's health becomes suboptimal. Additionally, our calculations do not include species-specific feeding behaviours and other possible sources of nutrients, such as osteophagy (Bredin et al., 2008). For example, smaller species may be able to select higher-nutrient plant species or plant parts in comparison to large bulk feeders (Clauss et al., 2013). Osteophagy is also commonly observed for several species at TKR, including giraffe, sable and kudu (Dylan Smith, Director of Research at TKR, personal communication). However, the congruence between our intake calculations and faecal P measurements, which would include other nutrient sources, suggests that P is indeed limiting for large herbivores.

Anthropogenic nutrient supplementation is only important for large herbivores if energy and protein requirements are adequate (McDowell, 1996). Without sufficient calories, large herbivores cannot utilise supplementary nutrients for metabolic functions, growth, or reproduction (Robbins, 2012). In some cases, nutrient supplementation without sufficient energy and protein can even be harmful to wildlife (Goff, 2018). For example, Van Niekerk and Jacobs (1985) found that P supplementation had a negative effect on feed intake and body mass change for cattle consuming low-quality diets in southern Africa, unless it was given in combination with both energy and protein supplements due to further burdening effects of P on an already unbalanced diet. Based on the faecal assessment for N conducted in this study, it appears that large herbivore grazers may not be able to utilise minerals from licks during the dry season due to a lack of dietary energy and protein. The mean dry season faecal N concentration for blue wildebeest of 12.6 g kg^{-1} falls below the threshold of potential concern equal to 14 g kg^{-1} as suggested by Wrench et al. (1997) (Fig. 4). In a focused study assessing the health of buffalo at TKR, Cromhout (2007) similarly found mean dry season faecal N concentrations below the threshold of potential concern at 10.8 g kg^{-1}. However, in the same study, Cromhout (2007) also demonstrated that the N concentration of palatable grass species at TKR increased by 42–82 % in the wet season, indicating that large herbivore grazers likely have sufficient energy/protein during this period. Based on our results, however, most mixed feeders and browsers will likely benefit from anthropogenic lick supplements throughout the year. The higher body condition scores of mixed feeders and browsers compared to grazers further corroborates this assertion (Fig. 5a).

Where animals have sufficient energy and protein, many studies have highlighted the role of supplementary macro-nutrients (e.g., P, Na) in rapidly increasing weight gain and reproductive success in domestic (Tait and Fisher, 1996; De Brouwer et al., 2000) and wild animals (Van der Waal et al., 2003; Milner et al., 2014). For example, a five-year study in the South African highveld found that P and Na supplementation for cattle during the wet season resulted in 18–27 % higher body mass, 75–144 % higher body condition score and 15–175 % higher bone P content (De Brouwer et al., 2000). Consequently, the substantial contribution of mineral and salt licks to daily P and Na intake found in our study may play an important role in the health of large herbivores at TKR, albeit in times of the year when sufficient energy can be obtained. Anthropogenic licks may be particularly important in helping grazers build sufficient body condition during the wet season to buffer catabolism during the dry season (McDowell, 1996), whilst mixed feeders and browsers, may benefit throughout the year (Van der Waal et al., 2003).

Although mineral licks contribute a smaller daily percentage of micronutrients, including Cu (0.2–6.7 %) and Zn (0.2–6.1 %), this may be a critical source for certain animal groups, which have elevated

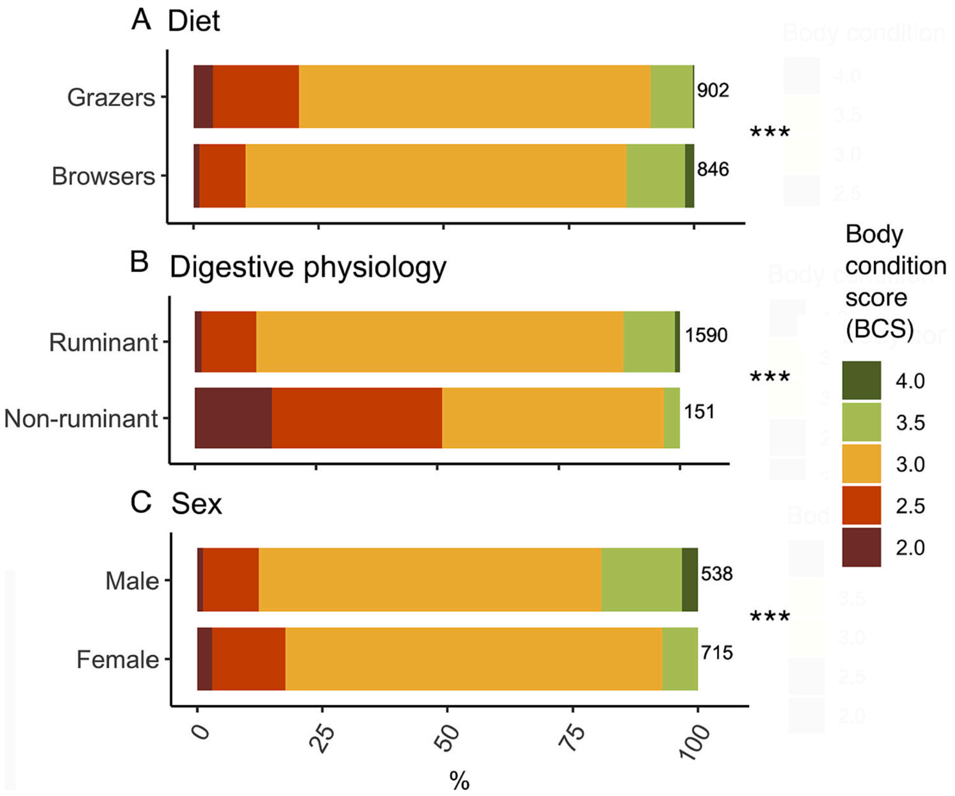

Fig. 5. Body condition scores for large herbivore (>10 kg) species at Tswalu Kalahari Reserve (TKR) split by diet, digestive physiology, and sex. Numbers next to each bar denote sample size for that group. *** denotes a statistically significant ($p < 0.001$) difference between groups using a Wilcoxon rank sum test.

demands due to antagonism of these nutrients with other elements. For example, the absorption rate of Cu in ruminants can become very low (<1 %) in environments where molybdenum (Mo), sulphur (S) and Fe are found in high concentrations (Suttle, 2010). Based on Mo and S concentration measurements at TKR by Webster et al. (2021) and Fig. 11.3 from Suttle (2010), the percentage of absorbable Cu in some ruminant species may be <3 %, indicating the potentially important role of anthropogenic mineral licks in satisfying requirements for these species. Similarly, high levels of Ca at TKR may reduce the absorption efficiency of Zn for hindgut-fermenters (Suttle, 2010). Given Zn-deficient animals would be expected to lose their appetite (Suttle, 2010), this may explain the lower dry-season body condition of non-ruminants compared to ruminants (Fig. 5b) and increased utilisation of mineral licks by this group (Fig. S4).

4.2. *Ecological implications of salt and mineral licks for conservation*

Supplemental provisioning of salt and mineral licks has several implications for nutrient-poor ecosystems worldwide. First, the geography of anthropogenic lick sites strongly influences local movement and congregation patterns of many large herbivore species, with concomitant implications for species coexistence, competitive behaviour, disease transmission and localised sites of high ecosystem impact (e.g., overgrazing; Priesmeyer et al., 2012). At broad-scales, mineral licks may also play a supporting role for resident individuals of species that would otherwise typically migrate, such as blue wildebeest or moose (Jones and Hanson, 1985; Knight et al., 1988). Second, nutrients gained from licks may have a strong influence on herbivore population density via changes to animal health, fertility and susceptibility to disease and predation (Suttle, 2010; Murray et al., 2016). Supplemental nutrient resources have been shown to increase body mass and fertility in livestock (De Brouwer et al., 2000) and birds (Shutt and Lees, 2021). In the case of TKR, it is therefore likely that the provision of salt and mineral licks, in combination with year-round access to artificial water sources (Robbins, 2012), contributes to population-level status of good health (see Section 4.1). We do note, however, that our study was conducted following a year of high rainfall (>500 mm yr^{-1} compared to 20-year average of ~360 mm yr^{-1}) and that our conclusions may differ during drought years when forage energy and protein availability is lower. Nevertheless, if Cu, Na, P or Zn are critically limiting for herbivore population size (Figs. 3 and 4), as has been shown in other areas of the Kalahari (Grant et al., 1996), we suggest that the provision of supplementary salt and mineral lick resources may have appreciably elevated large herbivore populations beyond the natural carrying capacity.

If so, what impact could this have for conservation goals and ecosystem integrity in the long term? Over the last 20 years, TKR has experienced gradually declining veld quality due to overgrazing and drought (Tokura et al., 2018; van Rooyen and van Rooyen, 2022). Between 1999 and 2022, the mean veld condition index, measured by 111 repeated sample plots across TKR, fell from 70 % to 30 %, where <40 % represents low grass cover with many unpalatable annual grasses and forbs (van Rooyen and van Rooyen, 2022). We hypothesize that the adopted management approach may have unintentionally contributed to this degradation by decoupling wildlife fecundity from nutrient-related feedbacks. If true, then the provision of anthropogenic salt and mineral licks is misaligned from TKR's stated goal of ecosystem restoration (https://tswalu.com/conservation-story/conservation/).

4.3. *Management options and future research*

Wildlife managers face challenges in providing supplementary nutrients for large herbivores via free-choice salt and mineral licks. On one hand, mineral and salt lick provision can rectify ethical issues related to animal husbandry and wildlife confinement. On the other, it may elevate herbivore populations beyond the long-term carrying capacity and place unsustainable pressure on the rest of the ecosystem. Managers must therefore first define what nutrient thresholds are appropriate to achieve reserve-specific conservation goals. We note that this may be challenging given that tourists often prefer to observe "healthier" animals (Dubois and Fraser, 2013), despite catabolism and death being natural processes (Robbins, 2012). For example, a rewilding experiment at Oostvaardersplassen, Netherlands, was terminated in 2018 due to public outcry over unacceptable levels of animal starvation (Theunissen, 2019). Each protected area will have associated idiosyncrasies, and assessments must be made on a location-by-location basis.

Shutt and Lees (2021) provide a unified theoretical framework for characterizing different forms of wildlife provisioning, with targeted or generalised provisioning providing either replacement or additional resources. Our study provides a predictive framework for quantifying the contribution of generalised resource provisioning to large herbivore communities with direct insights for management. For example, mineral lick provisioning at TKR may align more strategically with stated conservation goals if practiced in the form of 'targeted provisioning of replacement nutrients' only. Wildlife managers could stop providing licks during the dry season when low energy and protein availability prevents nutrient utilisation by grazers (see Section 4.1). Similarly, given that hunger for salt is currently considered the strongest driver of lick use (Suttle, 2010), the provision of only salt licks could be used to guide animal movements away from wildlife congregation sites without offering additional trace minerals, helping to reduce areas of high ecological degradation (Brown and Cooper, 2006; Priesmeyer et al., 2012). In contrast, providing only mineral licks (with a lower concentration of sodium and hence likely higher intakes) could be a way of increasing trace mineral supplementation in nutrient-poor sites where animal population growth rates are sub-optimal. Future improvements to our framework such as the explicit inclusion of forage nutrient phenology, species-specific diet intake and camera-trap monitoring across seasons will help refine estimates and better inform management decisions. To ensure that nutrient intake calculations are robust, animal health should be regularly monitored and lick provisions adjusted accordingly. Here, we compared nutrient intake with two non-invasive options for monitoring large mammalian herbivore health; faecal and body condition indicators. Other methods such as gut/tissue sampling, telemetry, stable isotopes, and direct behavioural observations may also be informative (Birnie-Gauvin et al., 2017).

Many protected areas are located in marginal environments (Joppa and Pfaff, 2009) which may suffer decreasing fertility over the coming century (Birnie-Gauvin et al., 2017). To reduce wildlife reliance upon mineral licks in these environments, managers should recalculate the long-term carrying capacity for their reserves (Milner et al., 2014). Lowering herbivore density will allow resident individuals to access higher quality resources via decreased intra- and inter-species competition (Van der Waal et al., 2003; Okita-Ouma et al., 2021). Herbivore populations can be decreased by off-site removal. However, this comes with associated costs of nutrient leaching (Abraham et al., 2021), which over long periods (e.g. decades) may result in declining ecosystem fertility. Alternatively, more balanced natural predation can regulate herbivore populations, whilst increasing landscape nutrient heterogeneity (Monk and Schmitz, 2022). Landscapes of fear generated by predators can additionally prevent prey from over-exploiting high-resource areas, including mineral lick sites (Abraham et al., 2023), which may further help regulate herbivore population levels and reduce ecosystem degradation associated with congregating behaviour.

5. Conclusion

In this study, we have shown that for a wildlife reserve in the Kalahari Desert, nutrients acquired from anthropogenic mineral licks can contribute considerably towards achieving herbivore nutrient intake requirements, particularly for larger-bodied species. Animals appear in good condition, yet over the last 20 years, TKR has experienced gradually declining forage quality (van Rooyen and van Rooyen, 2022). We suggest that ubiquitous mineral lick availability may have decoupled large herbivore fecundity and population growth from nutrient-related feedbacks, contributing to an artificial inflation of large herbivore abundance beyond the natural ecosystem carrying capacity. This mechanism has potential to degrade ecosystem integrity through overgrazing and habitat degradation. However, our study is observational, and can only show associations, not causation. Furthermore, the conclusions drawn in our study rely heavily on research conducted on the effects of salt and mineral licks for domestic livestock and white-tailed deer (Suttle, 2010; Milner et al., 2014). Yet, nutrient resources have been supplied in wildlife landscapes across the world for hundreds, if not thousands of years (Oro et al., 2013) and are increasingly being used to actively promote conservation goals (e.g. Felton et al., 2017; Simpson et al., 2020). Further experimental investigations examining the impact of mineral lick provision on ecosystem composition and function are required. Based on results presented here, it is clear that anthropogenic provision of mineral licks should be cautiously considered by wildlife managers aiming to conserve or restore natural processes in landscapes.

Ethical statement

All data were collected with the approval of the University of Pretoria Research and Animal Use and Care Committee (Reference NAS115/2021) and the South African Department of Agriculture, Land Reform and Rural Development 12/11/1/1/8(1933NC) and 12/11/1/1/8 A (1933NC) JD.

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CRediT authorship contribution statement

Andrew J. Abraham: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Ethan S. Duvall:** Formal analysis, Writing – review & editing. **Elizabeth le Roux:** Writing – review & editing. **Andre Ganswindt:** Conceptualization, Writing – review & editing. **Marcus Clauss:** Formal analysis, Writing – review & editing. **Christopher E. Doughty:** Writing – review & editing. **Andrea B. Webster:** Conceptualization, Methodology, Writing – review & editing.

Declaration of competing interest

Andrew Abraham reports financial support was provided by Tswalu Kalahari Reserve.

Andrea Webster reports financial support was provided by Tswalu Kalahari Reserve.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110149.

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