

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

Abstract

In nutrient-poor wildlife reserves it has become common-place to provide supplemental mineral resources for wildlife. Yet, the impacts of anthropogenic mineral supplementation on community-wide wildlife nutrition, behaviour and subsequent impact on ecosystem processes remain poorly understood. Here, we examine the contribution of anthropogenic mineral lick provision to wildlife nutrient intake across a community of large mammals (>10kg) in the southern Kalahari Desert. Based on predicted daily nutrient requirements and a faecal nutrient assessment, large herbivores appear deficient in phosphorus (P), sodium (Na) and zinc (Zn). For these nutrients, anthropogenic salt and mineral licks constitute an important (>10%) source of nutrient intake helping to reduce or overcome requirement deficits. Larger-bodied species disproportionately consumed licks ($p<0.01$), acquiring more nutritional benefits. A comprehensive assessment of animal body condition indicated that in general large herbivores display good health. However, bulk grazers, hindgut fermenters and females were more likely to display signs of malnourishment. We discuss how provisioning of anthropogenic mineral licks may be inflating large herbivore populations beyond the long-term carrying capacity of the reserve, with subsequent impacts for ecosystem integrity and herbivore population instability. Based on results presented here, it is clear that anthropogenic provision of mineral licks should be considered carefully by wildlife managers aiming to conserve or restore natural processes in conservation and rewilding landscapes.

22 1. Introduction

23 The nutritional status of wildlife directly influences animal health, fertility and susceptibility to
 24 disease and predation (Robbins, 1993; Milner et al., 2014). Consequently, human activities that limit
 25 wildlife access to nutrient resources can exert a strong control over ecosystem composition and
 26 function (Hobbs and Swift, 1985; Birnie-Gauvin et al., 2017; Abraham et al., 2022). For example,
 27 many protected areas (PAs) throughout the world are fenced to mitigate human-wildlife conflicts
 28 (Pekor et al., 2019), which prevents free movement of large-bodied animals and may limit access to
 29 essential resources such as food and water (Jakes et al., 2018). Particularly in oligotrophic
 30 environments, where these animals tend to have larger home ranges, fences can cause substantial
 31 nutritional stress (Boone and Hobbs, 2004).

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 33 To counter impeded access to adequate nutrition in fenced, oligotrophic PAs, wildlife managers
 34 often supply anthropogenic mineral licks (Milner et al., 2014; Murray et al., 2016; Simpson et al.,
 35 2020). The benefits of supplemental nutrition for animal health have been well understood in
 36 livestock and hunting landscapes for thousands of years (Theiler et al., 1924; Oro et al., 2013). In
 37 these settings, the aim is to maximise physical growth and population density of target species for
 38 increased harvest, protein or economic return (McDowell, 1996; Bartoskewitz et al., 2003). Similar
 39 motives exist in tourism landscapes, where increasing the health, density and encounter rate of
 40 wildlife via mineral provisioning can lead to enhanced viewing experiences for tourists (Dubois and
 41 Fraser, 2013; Cox and Gaston, 2018).

42
 43 While supplementing minerals in PAs has become common practice, it has largely retained the
 44 production-oriented approach inherited from its agricultural origins. Yet, the impacts of
 45 anthropogenic lick provision on community-wide wildlife nutrition, behaviour and subsequent
 46 impact on ecosystem processes have received little attention (Brown and Cooper, 2006; Milner et
 47 al., 2014). For example, in PAs where the aim is to preserve or restore natural processes, what
 48 quantity of anthropogenic mineral lick is the correct amount to provide? On one hand, too little
 49 provision may result in malnourished individuals that are susceptible to disease or predation, raising
 50 questions of ethical animal husbandry (Dubois and Fraser, 2013). On the other, excessive provision
 51 may result in exceptionally healthy animals that inflate population densities above the long-term
 52 carrying capacity of the ecosystem (Oesterheld et al., 1992; Milner et al., 2014). In the latter case,
 53 this may compromise the integrity of the PA due to issues of over-grazing or herbivore population
 54 instability (Boone and Hobbs, 2004; Milner et al., 2014). Accordingly, if anthropogenic licks are
 55 provided in PAs, it is important to ascertain which species/individuals consume the licks, what

contribution this makes to their required nutrient intake, and whether supplementation helps to reach conservation goals.

Here, we examine the contribution of anthropogenic mineral lick provision for wildlife nutrient intake across a large (>10kg) mammal community in the southern Kalahari Desert. Given this region is nutrient-poor (O'Halloran et al., 2010), mineral licks may form a critical part of nutrient intake for large vertebrate populations (Knight et al., 1988). Specifically, we aim to quantify the proportion of required nutrients that large mammalian herbivores acquire from anthropogenic salt and mineral licks compared to other primary sources of forage and water. We then assess what role these additional nutrients may have for wildlife health by undertaking two separate measures; (i) an assessment of faecal nutrient concentrations, and (ii) an assessment of animal body condition. Both measures have been widely employed for non-invasive assessments of wildlife health and can provide a holistic picture of nutrition status (Wrench et al., 1997; Ezenwa et al., 2009). Finally, we discuss the role that anthropogenic mineral provision may have for reaching conservation goals and how to ensure that wildlife management decisions are appropriate to reach these.

2. Methods

2.1 Study site

Tswalu Kalahari Reserve (TKR) is a 121,700 ha fenced wildlife reserve located at -27.26, 22.45 in the southern Kalahari Desert, South Africa (figure 1). 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) (figure 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; Cromhout, 2007; O'Halloran et al., 2010). As a result, wildlife managers at TKR provide supplementary nutrients in the form of anthropogenic ~62kg salt (Na) and ~25kg mineral (Ca, P, S, Co, Cu, I, Fe, Mg, Se, Zn) licks distributed throughout the reserve (figure 2; 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 figure 1). Once licks are consumed, they are immediately replenished ensuring constant availability throughout the year. In total, TKR provide 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, in this paper both sections together are considered together.

2.2 Large herbivore abundance

At TKR, large herbivore (>10kg) 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 SI text 1 for details and comparison to ground-based validation; Buckland et al., 1993). Large herbivore abundance estimates for the Greater Korannaberg and Lekgaba sections in 2021 are provided in SI table 1.

2.3 Large herbivore nutrient requirements

Nutrient requirements have been extensively studied in livestock (Suttle, 2010). However, less research has been conducted on wild ungulate species, which may have different nutrient demands (Robbins, 1993). In addition, specific requirements within a species may vary due to environmental (e.g. climate), reproductive state (e.g. pregnancy or lactation) or individual (e.g. age, sex, parasite load) differences (Robbins, 1993; Suttle, 2010). Here, we take a conservative approach and compare mean annual nutrient intake from forage, water and anthropogenic mineral licks at a population level to optimal requirements suggested by Lintzenich et al. (1997) for adult zoo animals at maintenance. This allows us to contextualise the contribution of anthropogenic mineral licks, but overlooks critical seasonal and individual differences. Importantly, however, Lintzenich et al. (1997) do include the influence of body size and digestive tract morphology on nutritional requirements, which potentially modify specific requirements in mammals (Clauss et al., 2013). For example, hindgut fermenters often require higher nutrient intake due to their lower digestive efficiency (Clauss et al., 2015). Here, we specifically focus on Ca, P, Na, Zn, iron (Fe) and magnesium (Mg),

which are all nutrients closely linked to health and reproduction in large mammals (Robbins, 1993; Suttle, 2010). Species-specific nutrient requirements were calculated using equation 1:

$$NI_{requirement_{i,j}} = \frac{RC_{i,j}}{0.9} * DMI_j \quad (\text{equation 1})$$

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 $\text{mg.g dry matter}^{-1}$ on a 90% dry matter basis for species j defined by Lintzenich et al. (1997), and DMI_j is dry matter intake estimated using the allometric relationship for field metabolic rate of $4.82 * \text{BM}^{0.734}$ and metabolizable energy of the diet for species j equal to 10 kJ.g DM^{-1} for hindgut fermenters and $11.5 \text{ kJ.g DM}^{-1}$ for ruminants from Nagy et al. (1999). Table 1 outlines species-specific mass, digestive physiology and daily nutrient intake requirements.

2.4 Large herbivore nutrient intake

In natural environments, large mammalian herbivores primarily acquire nutrients from forage and water (Robbins, 1993). Our aim here is to put nutrient acquisition from anthropogenic mineral licks at TKR into context when compared to other these major sources. Whilst geophagy (ingestion of soil) and osteophagy (ingestion of bone) are known contributors of nutrition for Kalahari herbivores (Knight et al., 1988; Holdo et al., 2002), we do not currently have estimates for these sources.

Natural forage intake: Plant nutrient content notably varies between grasses, forbs and woody plants (Kattage et al., 2021). Therefore to include diet differences, we first derived the contribution of C4 plants (i.e. grasses) to the diet of each species (see Table 1; Codron et al., 2007; Staver and Hempson, 2020). Nutrient concentrations for commonly-consumed plant species were then collated from studies previously conducted at TKR, representing seven C3 and six C4 species (Cromhout, 2007; Abraham et al., in prep, Webster et al., 2021; Prayag et al., 2020; Helary et al., 2012). Foliar concentration data from collated studies was, however, biased towards the dry season. In addition, the southern Kalahari experiences significant inter-annual climate variability (e.g. precipitation), which can influence nutritional quality (Skarpe and Bergstrom, 1987). To ensure that plant nutrient values reported at TKR are broadly representative of longer-term trends, we compared mean reported values at TKR to other sites in the southern Kalahari (table 2). In general, reported plant nutrient concentrations were similar to nearby sites for both C3 and C4 plants (table 2). We did, however, adjust excessively high reported values of Ca in C3 species at TKR from $30,765 \text{ mg.kg}^{-1}$ to $15,000 \text{ mg.kg}^{-1}$ to align with data reported from other sites. As herbivore diet quality generally scales

negatively with body mass (Clauss et al., 2013), we modified plant nutrient concentration by a quality factor for each species to account for selective foraging by smaller species (see table 1). Daily forage nutrient intake for an individual of each species was calculated using equations 2 and 3:

$$NI_{C3,i,j} = C_{C3,i} * DMI_j * (1 - \%C4_j) * S_j \quad (\text{equation 2})$$

$$NI_{C4,i,j} = C_{C4,i} * DMI_j * \%C4_j * S_j \quad (\text{equation 3})$$

Where $NI_{C3,i,j}$ and $NI_{C4,i,j}$ is the nutrient intake from C3 and C4 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 $\text{mg.g dry matter}^{-1}$ of C3 and C4 plants, DMI_j is dry matter intake for species j in g.day^{-1} (see equation 1), $\%C4_j$ is the percentage of C4 plants in the diet of species j and S_j is a forage selectivity factor for species j (ranging from highly selective, 1.4, to unselective, 1.0 – see table 1).

Water: Waterhole quality surveys have been conducted extensively at TKR over the period 2000-2021 (see SI text 2 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):

$$NI_{\text{water},i,j} = C_{\text{water},i} * 99 * BM_j^{0.9} \quad (\text{equation 4})$$

Where $NI_{\text{water},i,j}$ is the nutrient intake from water of nutrient i for an individual of species j in mg.day^{-1} , $C_{\text{water},i}$ 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 . Desert-adapted animals, however, often satisfy water consumption requirements through their diet rather than surface water (Kihwele et al., 2020). Consequently, the calculation of nutrient intake from water sources for herbivores at TKR is likely a conservative upper estimate.

Salt and mineral licks: To quantify nutrient intake from salt and mineral licks, we first analysed licks for nutrient concentration. 20g samples of salt ($n=5$) and mineral ($n=5$) licks were collected from TKR and individually pulverised. At the University of Pretoria's Soil Sciences Laboratory, 0.25-0.30g of each sample was weighed into microwave digestion tubes. 10 ml of Suprapur Nitric acid (65%) was added to each sample and samples were left to digest overnight prior to analysis for Ca, P, Na, Mg,

Fe, Zn concentration using a SPECRO GENESIS Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES). 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 for in the Greater Korannaberg (n=12) and Lekgaba (n=7) sections 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 (>10kg) present within the camera trap frame and the number of animals that physically made use of the salt and mineral licks. To ensure each camera trap contributed equally to data analysis, visitation rate from each camera trap was standardised /24hrs. Based on camera trap videos, we assume that 80% 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. We calculated individual daily nutrient intake from salt and mineral lick consumption using equations 5 and 6:

$$NI_{salt_lick_{i,j}} = C_{salt_lick_i} * M_{saltlick} * F * \frac{BM_j^{0.75} * CT_{salt_lick_j}}{\sum_{j=1}^j BM_j^{0.75}} * \frac{1}{A_j * 365} \quad (\text{equation 5})$$

$$NI_{mineral_lick_{i,j}} = C_{mineral_lick_i} * M_{mineral_lick} * F * \frac{BM_j^{0.75} * CT_{mineral_lick_j}}{\sum_{j=1}^j BM_j^{0.75}} * \frac{1}{A_j * 365} \quad (\text{equation 6})$$

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 $mg.g^{-1}$, 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 (>10kg) set to 0.8 (see above), BM_j is the body mass of species j (table 1), $CT_{salt_lick_j}$ and $CT_{mineral_lick_j}$ are the proportional use of salt and mineral licks by species j as determined by camera traps and A_j is the abundance of species j as determined by aerial counts.

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, 1993; 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 herbivore species in southern Africa, 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 minutes post-defecation) from three abundant ruminant species representing three feeding types; blue wildebeest (*Connochaetes taurinus*; obligate grazer), springbok (*Antidorcas marsupialis*; mixed feeder) and kudu (*Tragelaphus strepsiceros*; obligate browser). Faecal collection (60 per species; total n =180) was conducted coincident with camera trapping (July-September), 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 (v1.5x) for instrument control and data processing. We then used acid digestion and ICP-OES quantification described above to determine P, Ca, Na, Fe, Mg and Zn 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). 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). Similar thresholds of potential concern have not been established for micro-nutrients and thus we focus our faecal analysis on N and P only.

2.6 Large herbivore body condition

Nutrition status 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 SI text 3 and SI table 2 for method for details; Ezenwa et al., 2009).

Assessment was undertaken by an observer (AW) with >10 years professional experience observing wildlife in southern Africa. 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 Ethical statement

All data was 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.

3. Results

3.1 Contribution of anthropogenic mineral licks to herbivore nutrient requirements at TKR

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 5,722 utilising mineral licks. Lick site visits, salt lick use and mineral lick use relative to species abundance scaled positively with body mass (figure 3). This relationship was consistent between both the Greater Korannaberg and Lekgaba sections (SI figure 3). Buffalo (*Syncerus caffer*) relatively consumed salt licks the most (4.9x more regularly than predicted by their abundance), whilst plains zebra (*Equus quagga*) relatively consumed mineral licks the most (4.5x more regularly). Steenbok (*Raphicerus campestris*) very rarely used either salt or mineral licks, despite their high abundance at TKR (figure 3).

We calculated that many large herbivores at TKR consumed P, Na and Zn in amounts lower than required (figure 4). In general, grazers tended to be deficient in P, browsers deficient in Na and hindgut fermenters deficient in Zn. Salt and mineral licks constitute a substantial (>10%) component of daily intake of Na for all large herbivore species and of P for most large herbivores >100kg. Licks contributed >50% of daily Na intake for buffalo and eland (*Taurotragus oryx*) and >15% of daily P intake for buffalo, plains zebra and white rhino (*Ceratotherium simum*).

3.2 Assessment of large herbivore health at TKR

92% of kudu (browsers) and 100% of springbok (mixed feeders) faecal samples are above the N threshold of potential concern, suggesting that most individuals from these groups may have sufficient protein in their diet to utilise provisional nutrients acquired from anthropogenic salt and

mineral licks (figure 5). However, only 18% of blue wildebeest (grazer) faecal samples are above the critical N threshold of potential concern. Mean faecal P concentration is below the threshold of potential concern for blue wildebeest and kudu, whilst 43% of springbok samples are below the threshold of potential concern.

In total, 1865 BCS were obtained from TKR. Generally, large herbivores (>10kg) are in reasonable health with a mean BCS of 2.97. Using two sample t-tests, grazers (M = 2.92; SD = 0.31) display a statistically significant lower body condition than mixed feeders and browsers (M = 3.02; SD = 0.29), $t(1744) = 6.879$, $p < 0.001$ (figure 6a), hindgut fermenters (M = 2.68; SD = 0.39) display a statistically significant lower body condition than ruminants (M = 2.99; SD = 0.28), $t(165) = -9.51$, $p < 0.001$ (figure 6b), and females display a statistically significant lower body condition (M = 2.93; SD = 0.28) than males (M = 3.05; SD = 0.33), $t(1050) = -6.36$, $p < 0.001$ (figure 6c).

4. Discussion

4.1 Mineral licks as an important source of nutrients at TKR

Mean daily salt lick consumption varies from 0.003 g.day⁻¹ (steenbok) to 16.7 g.day⁻¹ (buffalo), whilst mineral lick consumption varies from 0.02 g.day⁻¹ (steenbok) to 68.4 g.day⁻¹ (white rhino). These values compare similarly to the rates of anthropogenic lick consumption in other non-pastoral systems (e.g. ~18 g.day⁻¹ by white-tailed deer (*Odocoileus virginianus*) in Louisiana, USA (Schultz and Johnson, 1992). However, values are considerably lower than for livestock farming in low-nutrient environments, where lick site density is generally higher and predators are absent (e.g. 135±55 g cattle⁻¹ day⁻¹; Tait and Fisher, 1996).

Based on the theoretical daily nutrient requirement calculations and the faecal nutrient assessment conducted in this study, many large herbivores (>10kg) at TKR appear deficient in P, Na and Zn. For these nutrients, anthropogenic salt and mineral licks constitute an important (>10%) source of nutrient intake helping to reduce or overcome requirement deficits (figure 4). This is especially true for larger-bodied species that consume licks disproportionately (figure 3) and individuals that have elevated nutrient demands (e.g. pregnancy, lactation, juvenile; Suttle, 2010). It is important to note that the data used to estimate mineral requirements for this study (i.e. Lintzenich et al., 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 other possible sources of nutrients for large herbivores at TKR including geophagy from natural mineral licks (Knight et al., 1988) and osteophagy (Bredin et al., 2008). If consumed at high

rates, these alternative sources may offset the importance of anthropogenic mineral licks for species to acquire sufficient nutrient intake. Whilst geophagy is rarely seen at TKR, osteophagy is more commonly observed for several species including giraffe (*Giraffa camelopardalis*), sable (*Hippotragus niger*) and kudu (*Tragelaphus strepsiceros*) (Dylan Smith, Director of Research at TKR, personal communication). Bones, which have high P concentrations, may therefore provide an additional important P resource, especially for species with large skeletons, which increases P demand (Bredin et al., 2008).

Liebig's Law of the Minimum suggests that 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 and reproduction (Robbins, 1993). In some cases, additional nutrient intake from anthropogenic sources without sufficient energy and protein can even be harmful to wildlife. For example, in a factorial study examining the effect of energy, protein and P supplements on cattle fed low-quality forage in southern Africa, van Niekerk and Jacobs (1985) found that P supplementation had a negative effect on feed intake and body mass change, 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) (figure 5). 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. Values this low indicate that some grazer individuals may struggle to maintain rumen fermentation due to inadequate nutrition for rumen microbes (Grant et al., 2000). However, in the same study, Cromhout (2007) also demonstrates that the N concentration of palatable grass species at TKR increases by 42-82% in the wet season, indicating that large herbivore grazers likely have sufficient energy/protein during this period to benefit from anthropogenic licks. Based on the results presented here, the majority of mixed feeders and browsers will, however, likely benefit from anthropogenic lick supplements throughout the year. The higher body condition scores of mixed feeders and browsers compared to grazers corroborates this assertion (figure 6a).

Where animals have sufficient energy and protein, many studies have highlighted the role of supplementary nutrients for rapidly increasing weight gain and increasing 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 significant P and Na supplementation of beef cattle during the wet summer 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 salt and mineral licks to daily P and Na intake found in this study may play an important role for the health of large herbivores at TKR, albeit in times of the year when sufficient energy can be obtained. For grazers, anthropogenic licks may help individuals quickly build sufficient body condition during the wet season to buffer catabolism during the dry season (McDowell, 1996), whilst for mixed feeders and browsers licks may provide an important source of nutrients throughout the year (van der Waal et al., 2003). Although mineral licks contribute a smaller daily percentage of Zn (0.1-5.2%), this may be a critical source for hindgut fermenters, which have elevated demands due to antagonism of Zn with phytate reducing absorption efficiency for this group (Suttle, 2010). Zn-deficient animals tend to lose their appetite, which may help explain the considerably lower dry-season body condition of hindgut fermenters compared to ruminants (figure 6b).

4.2 Ecological implications of salt and mineral licks for conservation at TKR

Supplemental provision of salt and mineral licks at TKR has several ecological implications. First, the geography of anthropogenic lick sites strongly influences the movement and congregation patterns of many large herbivore species, with concomitant implications for species interactions, coexistence and localised sites of ecosystem impact (Priesmeyer et al., 2012). Second, nutrients gained from licks may have a strong influence on wildlife health, fertility and susceptibility to disease and predation (Suttle, 2010; Murray et al., 2016). In this study, we find that large mammalian herbivores generally display good body condition, despite our intake calculations and dry-season faecal assessments indicating deficiencies in P, Na and Zn (figures 4 and 5). Evidently, while these nutrients are low, they do not appear critically limiting for animal health. It is likely that the provision of salt and mineral licks, in combination with year-round access to artificial water sources (Robbins, 1993), contributes to this 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 ($>500 \text{ mm yr}^{-1}$ compared to 20-year average of $\sim 360 \text{ mm yr}^{-1}$) and that our conclusions may differ during drought years when forage energy and protein availability is lower. Finally, wildlife act as important vectors of nutrient transport. Modifications to wildlife nutrient intake by anthropogenic mineral licks may influence the concentration and stoichiometry of nutrients across the reserve through animal-mediated lateral transport of elements, with concomitant impacts for wider ecosystem processes (Abraham et al., 2022).

In the absence of high rates 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 can lead to lower body condition and resulting recruitment rates (van der Waal et al., 2003; Lane et al., 2014). Therefore, if P, Na or Zn are critically limiting for herbivore population size at TKR, could the provision of supplemental salt and mineral lick resources appreciably elevate 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 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). Is it possible that the adopted management approach has unintentionally contributed to this degradation by decoupling wildlife health from nutrient-related feedbacks?

The southern Kalahari is a fragile ecosystem, whereby elevated herbivore population densities can have long-lasting impacts on vegetation diversity (Tokura et al., 2018). Field and remote-sensing studies at TKR have suggested that more effective predator control of large herbivore populations can help maintain vegetation productivity and diversity (Tokura et al., 2018; Makin et al., 2018). However, in the absence of sufficient predator regulation of herbivore populations in the Greater Korannaberg section, wildlife removals are conducted ($\sim 230\text{kg live biomass km}^{-2} \text{ year}^{-1}$), resulting in a substantial loss of nutrients from the landscape (Abraham et al., 2021). As a result, the provision of salt and mineral licks may inadvertently be generating a management conundrum, whereby licks help herbivore populations exceed the natural carrying capacity of TKR, resulting in ecological degradation and the need for off-site wildlife removal. This management process in turn leaches nutrients from the wider landscape with implications for ecosystem fertility and stoichiometry (Abraham et al., 2021), encouraging increased reliance of wildlife on mineral licks. If this hypothetical scenario is true, then the provision of anthropogenic salt and mineral licks may be 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 animals via free-choice salt and mineral licks. On one hand, this management strategy can rectify ethical issues related to

animal husbandry. But on the other, it may elevate herbivore populations beyond the long-term carrying capacity with possible ecosystem-wide degradation (Felton et al., 2017). Each protected area will have associated idiosyncrasies, and assessments must be made on a location-by-location basis.

To ensure that provision of anthropogenic salt and mineral licks aligns with conservation goals, managers should seasonally assess nutrient levels from various resource pools including forage, water and soil. Where inter-annual variability of nutrient resources is high (e.g. due to climate change, anthropogenic disturbance or migratory/invasive species; Birnie-Gauvin et al., 2017), assessments should be undertaken more frequently. Our study provides a framework to quantify the contribution of different nutrient resource pools to wildlife diet. However, future improvements to this framework such as species-specific forage intake and camera-trap monitoring across seasons will help refine estimates. Importantly, future assessments must define what nutrient thresholds are appropriate to achieve conservation goals, balancing the needs of animal health while restoring natural processes. We note that this may be a challenge for wildlife managers as tourist often prefer to observe “healthier” animals (Dubois and Fraser, 2013), despite catabolism and death being natural processes (Robbins, 1993). For example, a rewilding experiment at Oostvaardersplassen, Netherlands, was terminated in 2018 due to public outcry over unacceptable levels of animal starvation (Theunissen, 2019). Here, we suggest that based on calculated nutrient deficiencies, only essential nutrients that correct wildlife deficiencies should be available when required. For example, at TKR, managers should consider whether licks are required during the dry season when energy and protein availability limits nutrient utilisation of large herbivore grazers (see section 4.1). This will decrease wildlife congregations at lick sites, reducing areas of high ecological degradation (Brown and Cooper, 2006; Priesmeyer et al., 2012). To ensure that nutrient intake calculations are robust, managers should regularly monitor the health of animals and adjust lick provision accordingly. Here, we have presented two non-invasive options for managers to monitor large mammalian herbivore health using faecal and body condition indicators. Other methods such as gut/tissue sampling, telemetry, stable isotopes and direct behavioural observations could also be used (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 reserve (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; Gann et al., 2016; 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 Schmidt, 2021) and creating additional nutrient resources such as bones for osteophagy (Bredin et al., 2008). Landscapes of fear generated by predators can additionally prevent prey from over-exploiting high-resource areas, including mineral lick sites (Link et al., 2010), which may further help regulate herbivore population levels and reduce ecosystem degradation associated with congregating behaviour.

In this study, we have shown that for a wildlife reserve in the Kalahari Desert, nutrients acquired from anthropogenic licks can contribute significantly to herbivore nutrient intake requirements, particularly for larger-bodied species. Simultaneously, animals appear in good health, indicating that current wildlife management practices may play a role in artificially inflating populations beyond the natural ecosystem carrying capacity in the absence of mineral licks. This mechanism has potential impacts on ecosystem integrity through overgrazing and habitat degradation. This is, however, an observational study 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 carefully considered by wildlife managers aiming to conserve or restore natural processes in these conservation and rewilding landscapes.

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TABLES

Table 1. Characteristics and nutrient requirements for maintenance in ungulates resident at Tswalu Kalahari Reserve. Body mass values taken from Hempson et al. (2015), dietary C4 % from ^aCodron et al. (2006), ^bCodron et al. (2007), ^cStrauss (2015) and ^dStaver and Hempson (2020) and nutrient requirements from Lintzenich et al. (1997).

Species	Mass (kg)	Digestive physiology	Mean C4 in diet (%)	Selective feeding	Intake requirement (mg day ⁻¹)					
					Ca	P	Na	Mg	Fe	Zn
White rhino (<i>Ceratotherium simum</i>)	2196	Hindgut fermenter	90.0 ^d	1.0	43530	32650	16930	15240	780	780
Giraffe (<i>Giraffa camelopardalis</i>)	1118	Ruminant	5.0 ^d	1.0	17290	11530	6400	10380	310	170
Black rhino (<i>Diceros bicornis</i>)	1000	Hindgut fermenter	9.0 ^b	1.0	24440	18330	12200	8500	440	440
Eland (<i>Taurotragus oryx</i>)	511	Ruminant	11.8 ^d	1.1	9740	6490	3610	5840	180	100
Buffalo (<i>Syncerus caffer</i>)	486	Ruminant	94.0 ^d	1.1	9390	6260	3480	5630	170	90
Plains zebra (<i>Equus quagga</i>)	280	Hindgut fermenter	92.0 ^d	1.1	9610	7210	3740	3360	170	170
Mountain zebra (<i>Equus zebra</i>)	279	Hindgut fermenter	90.0 ^c	1.1	9560	7170	3720	3350	170	170
Roan (<i>Hippotragus equinus</i>)	264	Ruminant	96.8 ^d	1.2	6000	4000	2200	3600	110	60
Blue wildebeest (<i>Connochaetes taurinus</i>)	220	Ruminant	95.0 ^d	1.2	5250	3500	1940	3150	90	50
Sable (<i>Hippotragus niger</i>)	211	Ruminant	96.5 ^d	1.2	5080	3390	1880	3050	90	50
Gemsbok (<i>Oryx gazelle</i>)	204	Ruminant	85.7 ^d	1.2	4960	3300	1840	2970	90	50
Kudu	202	Ruminant	4.8 ^d	1.2	4930	3290	1830	2960	90	50

<i>(Tragelaphus strepsiceros)</i>										
Red hartebeest <i>(Alcelaphus buselaphus)</i>	150	Ruminant	99.3 ^d	1.2	3970	2640	1470	2380	70	40
Warthog <i>(Phacochoerus africanus)</i>	76	Hindgut fermenter	91.0 ^b	1.2	3680	2760	1430	1290	70	70
Impala <i>(Aepyceros melampus)</i>	49	Ruminant	54.3 ^d	1.3	1740	1160	650	1050	30	20
Springbok <i>(Antidorcas marsupialis)</i>	35	Ruminant	23.0 ^d	1.3	1370	910	510	820	20	10
Baboon <i>(Papio ursinus)</i>	30	Hindgut fermenter	30 ^a	1.3	1860	1400	720	650	30	30
Common duiker <i>(Sylvicapra grimmia)</i>	17	Ruminant	7.5 ^d	1.4	800	530	300	480	10	10
Steenbok <i>(Raphicerus campestris)</i>	11	Ruminant	13.3 ^d	1.4	590	390	220	350	10	10

Table 2. Mean values [range in brackets] of nutrient concentrations from sources at Tswalu Kalahari Reserve. For comparison, forage nutrient concentrations in the southern Kalahari are provided from Skarpe and Bergstrom (1987), Tolsma et al. (1987), Stepelberg et al. (2008) and Theart (2015). Values from Tolsma et al. (1987) were extracted using WebPlotDigitizer (<https://apps.automeris.io/wpd/>).

Source	Location	Ca (mg kg ⁻¹)	P (mg kg ⁻¹)	Na (mg kg ⁻¹)	Mg (mg kg ⁻¹)	Fe (mg kg ⁻¹)	Zn (mg kg ⁻¹)
C4 plants	Tswalu	3727 [2000-7600]	568 [300-1000]	345 [164-680]	2454 [500-11200]	194 [83-475]	16 [5-35]
	Skarpe and Bergstrom (1987)	3406 [2900-3956]	768 [571-975]				
	Tolsma et al. (1987)	8733 [2237-19635]	956 [123-2543]		2671 [425-6450]	440 79-1062]	
	Stepelberg et al. (2008)	6874 [6233-7213]	900 [567-1350]				
C3 plants	Tswalu	30765 [29300-32230]	1460 [1440-1480]	176 [85-400]		301 [175-530]	14 [3-25]
	Skarpe and Bergstrom (1987)	12235 [7667-24000]	1308 [550-2500]				
	Tolsma et al. (1987)	16160 [8056-44850]	1607 [712-2454]	115 [11-193]	2347 [1118-4155]	167 [56-391]	24 [13-52]
	Stepelberg et al. (2008)	15812 [9900-22950]	1378 [825-1967]				
	Theart (2015)	16450 [7450-26480]	1170 [750-1870]				20 [13-47]
Water	Tswalu	38 [5-150]	0.17 [0-1.67]	24 [6-70]	19 [3-91]	0.06 [0-0.7]	0 [0-0.0001]
Anthropogenic salt lick	Tswalu	4133 [4025-4194]	74 [13-178]	191979 [188319-196499]	143 [74-200]	103 [46-200]	0.7 [0.2-1.1]
Anthropogenic mineral lick	Tswalu	83262 [77000-86897]	36132 [29869-44291]	55284 [46159-60635]	3287 [2867-3794]	1370 [1336-1398]	181 [152-200]

FIGURES

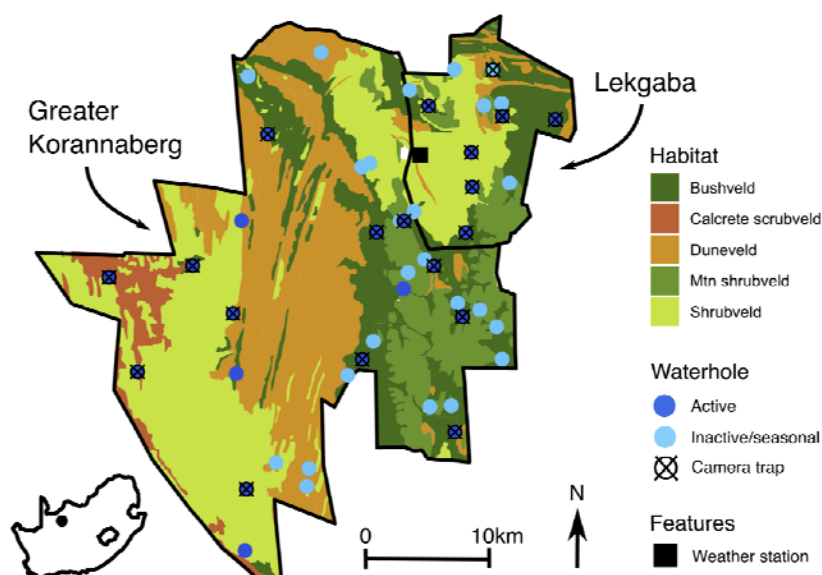
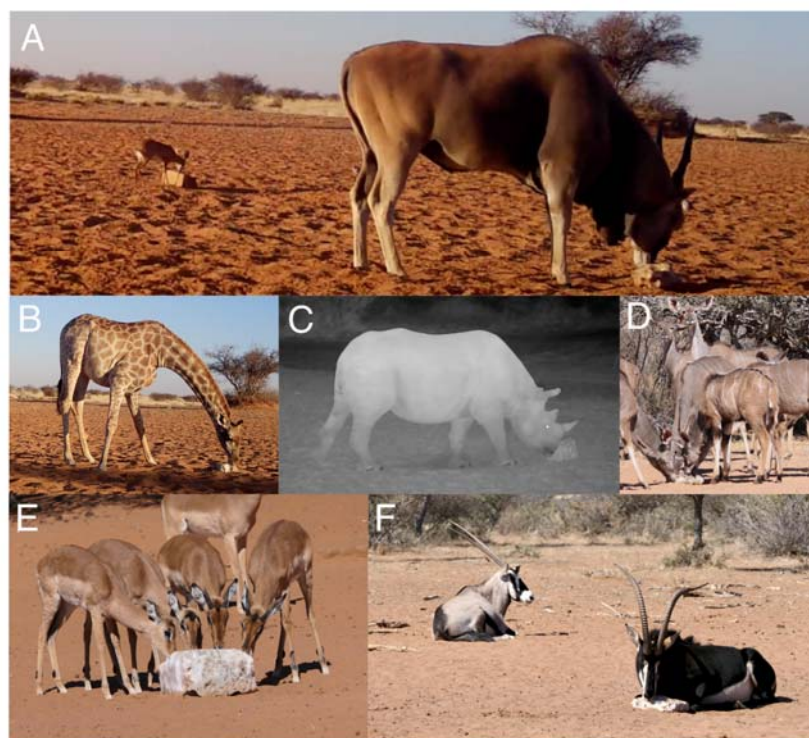
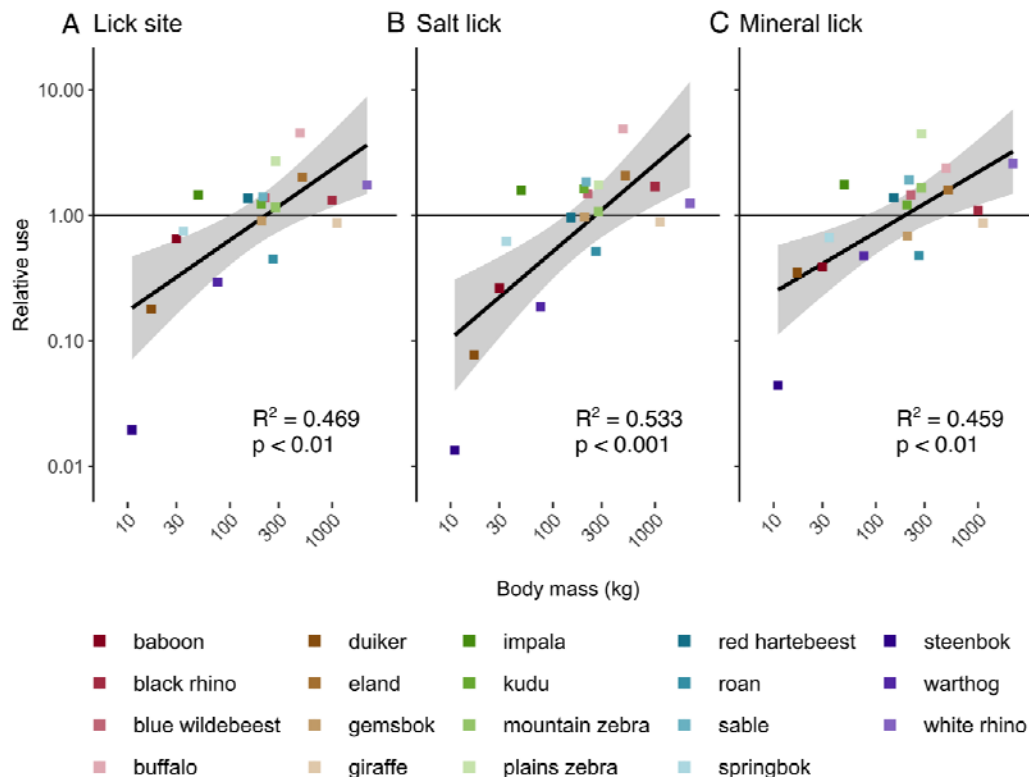


Figure 1. Tswalu Kalahari Reserve (TKR), South Africa, highlighting the Greater Korannaberg and Lekgaba sections, major habitat types (van Rooyen and van Rooyen, 2022) and the location of waterholes. Sites where camera traps were placed at salt and mineral licks to observe utilisation by large herbivores (>10kg) are denoted.



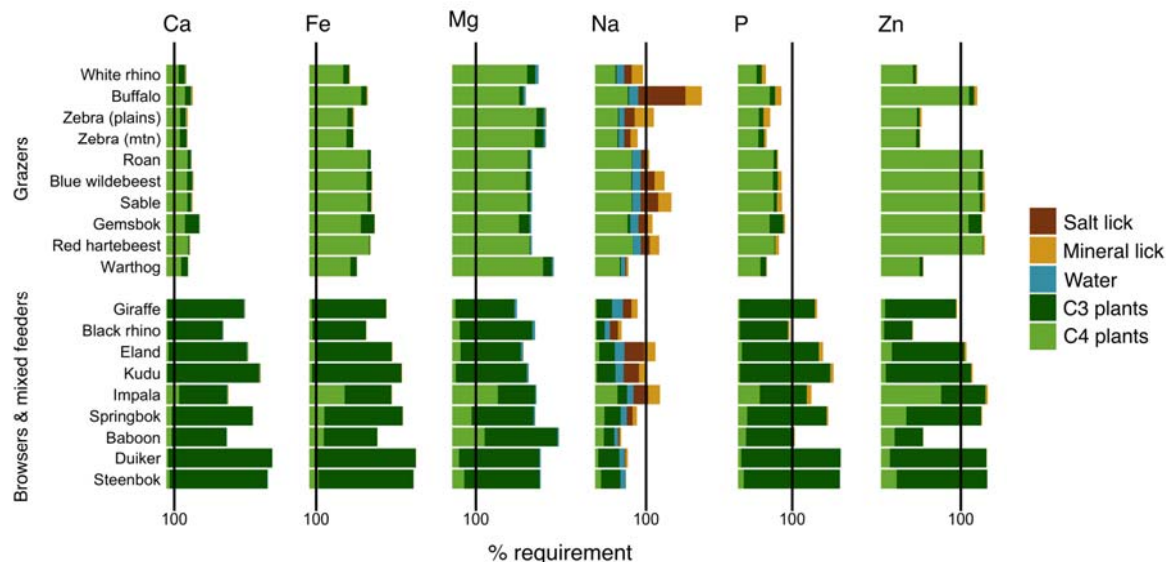
10

11 **Figure 2.** Salt and mineral lick consumption by (A) steenbok (*Raphicerus campestris*) and eland
12 (*Taurotragus oryx*), (B) giraffe (*Giraffa camelopardalis*), (C) black rhino (*Diceros bicornis*). (D) kudu
13 (*Tragelaphus strepsiceros*), (E) impala (*Aepyceros melampus*), and (F) gemsbok (*Oryx gazelle*) and
14 sable (*Hippotragus niger*) at Tswalu Kalahari Reserve (TKR). Photos taken by A. Abraham and A.
15 Webster.

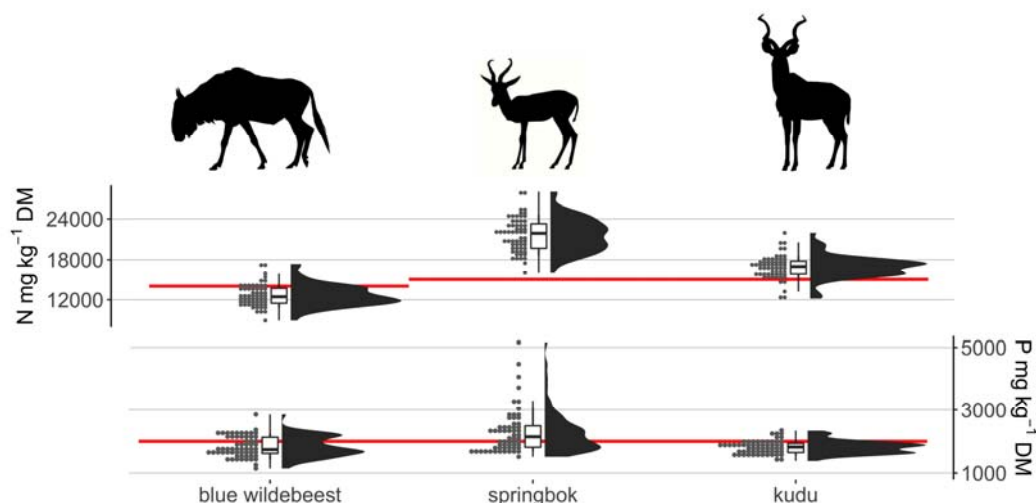


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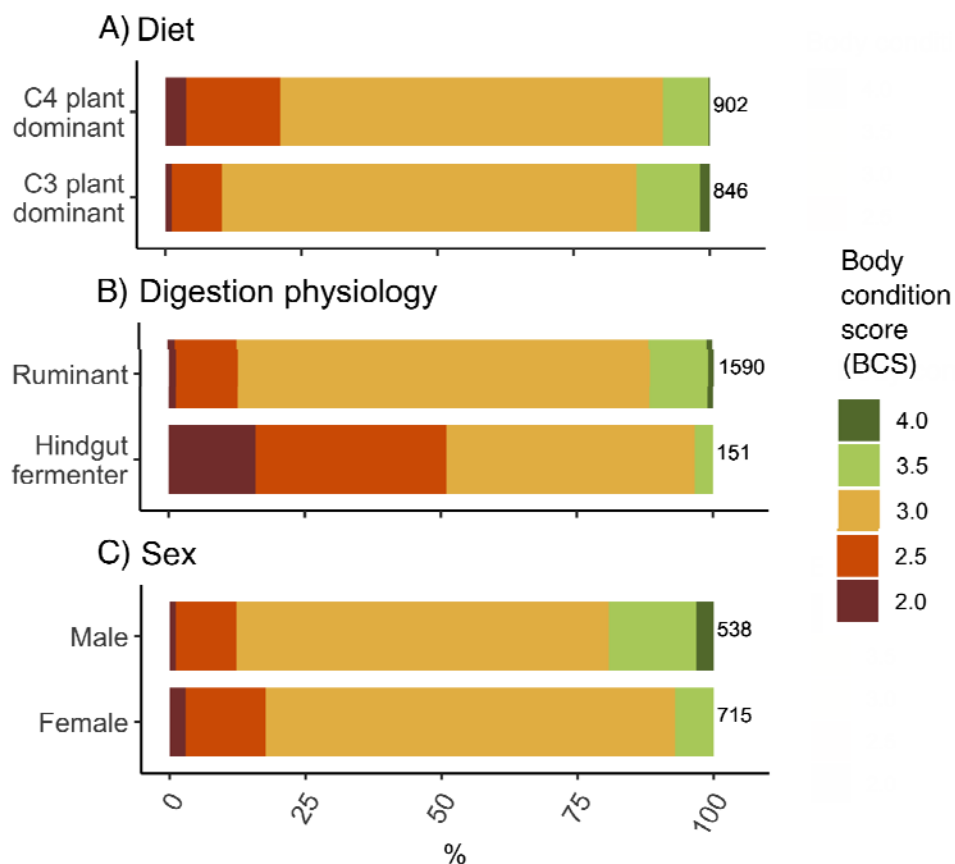
17 **Figure 3.** Relative visitation of large herbivores to anthropogenic lick sites (A), and direct use of salt
18 (B) and mineral (C) licks compared to abundance at Tswalu Kalahari Reserve (TKR). Note that the y-
19 axis is scaled log₁₀, where values >1 represent more visitations of licks than expected based on
20 species abundance and values <1 represent fewer visitations than expected. Trendlines represent a
21 generalised-least squares model fit for all herbivores.



22
23 **Figure 4.** Daily intake of calcium (Ca), iron (Fe), magnesium (Mg), sodium (Na), phosphorus (P) and
24 zinc (Zn) from different nutrient pools by large herbivores (>10kg) at Tswalu Kalahari Reserve (TKR).
25 Vertical lines represent daily nutrient requirements for adult individuals at maintenance as
26 suggested by Lintzenich et al. (1997).



27
28 **Figure 5.** Faecal macro-nutrient concentrations of nitrogen (N) and phosphorus (P) for blue
29 wildebeest (*Connochaetes taurinus*; obligate grazer), springbok (*Antidorcas marsupialis*; mixed
30 feeder) and kudu (*Tragelaphus strepsiceros*; obligate browser) resident at Tswalu Kalahari Reserve
31 (TKR). Red lines represent minimum faecal nutrient thresholds below which large mammalian
32 herbivores begin suffering growth and reproductive issues. The N threshold is 14,000 mg kg⁻¹ for
33 grazers and 15,000 mg kg⁻¹ for mixed feeders and browsers. The P threshold is 2,000 mg kg⁻¹ for all
34 species. Note that faeces were collected in the dry season (July-September) when nutrient stress is
35 typically greatest.



36
37 **Figure 6.** Body condition scores for large herbivore (>10kg) species at Tswalu Kalahari Reserve (TKR)
38 split by diet, digestive physiology and sex groups. Numbers next to each bar denote sample size for
39 that group.