

LARGE PREDATORS CAN MITIGATE NUTRIENT LOSSES ASSOCIATED WITH OFF-SITE REMOVAL OF ANIMALS FROM A WILDLIFE RESERVE

Running title: Wildlife removal and nutrient loss

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ABSTRACT

1. Animals concentrate key nutrients in their bodies. In fenced wildlife reserves where nutrient input and/or retention is low, the off-site removal of animals may constitute a significant loss of nutrients for the ecosystem.
2. Here we add wildlife capture and removal into the phosphorus (P) and calcium (Ca) budget for a 121,700 ha fenced game reserve located in the southern Kalahari. We then use faecal P concentrations from 11 mammal herbivores >10 kg as an indicator of potential nutrient stress in this system to investigate if the implications of nutrient loss via off-site wildlife removal may be cause for concern. Finally, we assess the role of natural predation as a mechanism to minimise the need for wildlife removal and concomitant nutrient loss.
3. During the period 2009-2018, mean loss of P and Ca via wildlife removal was 2.9 and 6.2 kg km⁻² yr⁻¹ respectively. This compares to 1.0 and 2.1 kg km⁻² yr⁻¹ of P and Ca added via the provision of mineral licks. If it is assumed that natural fluxes of these elements are in steady state, then anthropogenic activities have resulted in a net deficit of 18.5 kg km⁻² of P and 40.6 kg km⁻² of Ca over the decade.
4. We found that dry season herbivore faecal P concentrations are close to or below a widely cited minimum threshold of 2000 mg kg⁻¹, below which most vertebrates begin suffering growth and reproductive issues. Large animals were more likely to be under this threshold. Prolonged continuation of off-site wildlife removal may result in nutrient losses that can lead to long-term ecological degradation. Natural predation levels were, however, found sufficient to mitigate the need for wildlife removal and present a management strategy whereby herbivore populations can be regulated without a loss of nutrients.
5. *Synthesis and applications:* We find that the capture and permanent removal of large-bodied animals from wildlife reserves can be a significant cause of nutrient loss. Over time, in sites where nutrient input and/or retention is low, this may contribute to nutritional stress for remaining resident animals. Where possible, holistic management strategies that promote the retention of animals and carcasses within the reserve - such as the reintroduction of large carnivores - should be preferred.

TRANSLATED ABSTRACT (isiXhosa)

1. Izilwanyana ziqokelela ndawonye izondlo ezingundoqo emizimbeni yazo. Kwithanga elibiyelweyo lokugcina izilwanyana zasendle apho igalelo lezondlo okanye ukugcinwa kwezondlo kuphantsi, ukususwa ngaphandle kwethanga kwezilwanyana kusenokwenza ilahleko ebalulekileyo yezondlo kwindalo.
2. Apha sidibanisa ukubanjwa nokususwa kwezilwanyana zasendle kumyinge we-phosphorus (P) kunye ne-calcium (Ca) kwithanga lwezilwanyana zasendle elinesiza esiyi 121,700 ha elifumaneka emazantsi eKalahari. Sisebenzise ke iphosphorus efumaneka ebulongweni bezilwanyana ezanyisayo ezilishumi elinanye, ezibunzima bungaphezulu kweshumi lwekilograms njengesalathisi soxinizelelo lwezondlo olunokubakho koluhlobo lwethanga xa besiphanda ukuba ukuchaphazeleka koxinizelelo lwezondlo ngenxa yokususwa ngaphandle kwethanga kwezilwanyana kunokuba ngunobangela wenkxalabo. Okokugqibela, sivavanya indima yokutyiwa kwezilwanyana zezinye njengesixhobo esingasetyenziswa ukunciphisa isidingo sokususwa kwezilwanyana zasendle kumathanga wazo ehambelana kunye nokulahleka kwezondlo.
3. Ngexesha lika 2009 ukuya kunyaka ka 2018, ilahleko yephosphorus ne-calcium ngenxa yokususwa kwezilwanyana zasendle kumathanga wazo ibingumlinganiselo ongangesithathu ($2.9 \text{ kg km}^{-2} \text{ yr}^{-1}$) kwiphosphorus nesithandathu ($6.2 \text{ kg km}^{-2} \text{ yr}^{-1}$) kwicalcium. Oku kuthalekiswa kumlinganiselo omnye ($1.0 \text{ kg km}^{-2} \text{ yr}^{-1}$) wephosphorus kunye nemibini ($2.1 \text{ kg km}^{-2} \text{ yr}^{-1}$) yecalcium ezongezwe lubonelelo lweemitha zezimbiwa. Ukuba kucingelwa ngaba ukubhobhoza ngokwendalo kwezizinto kukwimeko ezinzileyo, ithetha ukuthi lonto imisebenzi eyenziwa ngabantu ephazamisa indalo ibangele intsilelo eninzi, engumlinganiselo weshumi elinethoba (18.5 kg km^{-2}) lwephosphorus namashumi amane ananye e-calcium (40.6 kg km^{-2}) kwiminyaka elishumi.
4. Sifumanise ukuba iphosphorus kubulongwe bezilwanyana ezanyisayo obuqokelelwe ngexesha lonyaka ekome ngalo isondele okanye ingezantsi kumyinge obekiweyo ngokubanzi wamawaka amabini (2000 mg kg^{-1}), myinge lowo ongezantsi othi wenze uninzi lwezilwanyana ezinomqolo ziqale ukukhula ngokubandezeleka kuchaphazeleke nemicimbi yokuzala. Izilwanyana ezinkulu bekusenzeka ukuba zibengezantsi kwalomyinge. Ukuqhubeka ixesha elide kokususwa kwezilwanyana zasendle kumathanga wazo kunobangela ilahleko yezondlo engakhokelela ekonakaleni kwendalo ixesha elide. Nangona kunjalo amanqanaba okutyiwa kwezilwanyana zezinye afunyenwe onele ukunciphisa isidingo sokususwa kwezilwanyana zasendle

kumathanga wazo kwaye ivelisa iqhinga lolawulo apho izilwanyana zinokulawulwa ngaphandle kokulahleka kwezondlo.

5. *Indibanisela noncedo: Sifumanisa ukuba ukubanjwa nokususwa ngokusisigxina kwezilwanyana zasendle kumathanga wazo kunokuba ngunobangela wokulahleka kwezondlo. Emva kwexesha elide, emathangeni apho igalelo okanye ukugcinwa kwezondlo kuphantsi kungenza uxinzelelo lwezondlo kwizilwanyana ezishiyekileyo. Apho kunokwenzeka, izicwangciso zolawulo olubanzi olukhuthaza ukugcinwa kwezilwanyana kunye nezidumbu ngaphakathi emathangeni - njengokungeniswa kwakhona kwezilwanyana ezitya ezinye- kokona kufanele kukhethwe.*

Keywords: biogeochemistry, calcium, carnivore, nutrient cycles, phosphorus, skeleton, wildlife management.

1. INTRODUCTION

Much of the land surface of earth is scarce in one or more nutrients vital for sustaining life (Sillanpää, 1982). Consequently, there is extensive documentation of behavioural adaptations by wild vertebrates that help them acquire sufficient nutrients, including seasonal migrations (McNaughton, 1990), geophagy (Holdo et al., 2002) and selective diet choices (Rothman et al., 2006). However, today many wildlife reserves are fenced or geographically isolated due to the presence of geophysical and/or anthropogenic barriers such as urban and agricultural areas. This can prevent vertebrates from sustaining their required nutrients, leading to seasonal or chronic nutrient stress (Thornton, 2002). Consequently, in nutrient-poor areas, wildlife managers often provide supplementary mineral licks or access corridors to high-nutrient regions (Newmark, 1993; Bothma and Du Toit, 2010).

Whilst vertebrate populations are constrained by the local availability of nutrients, a growing body of research demonstrates that animals play an important role in altering nutrient concentration geographies themselves. Through the accumulation and dispersal of nutrients in their bodies and excreta, vertebrate populations can provide a critical supply of allochthonous nutrient subsidies between ecosystems (reviewed in Subalusky and Post, 2018 and McInturf et al., 2019). Accordingly, extinctions, population reductions and the presence of anthropogenic barriers may have also reduced a critical input of important nutrients such as nitrogen (N) phosphorus (P), calcium (Ca) and sodium (Na) by wild, free-roaming vertebrates in marine and terrestrial environments (Roman et al., 2014; Doughty et al., 2016).

However, whilst much research has addressed the role of animals as important vectors of nutrient input within and between ecosystems, less effort has investigated their role as vectors of nutrient loss. In a pan-tropical assessment, Brodie and McIntyre (2019) found that the removal of P in the bodies of wild vertebrates hunted for bushmeat could constitute an important flux leaving the system. In some sites, they reported that P losses from hunting were >10 times that arriving from atmospheric deposition, which represents the primary input of P to those ecosystems. Similarly, Flueck (2009) reported P losses in the bodies and faeces of migrating red deer (*Cervus eleaphus*) from the Swiss National Park, Switzerland, equal to P fertilisation rates in many agricultural systems. Wildlife reserves cannot, however, simply replace lost nutrients via the application of nutrient fertilisers. Firstly, wildlife reserves often cover vast areas making fertilisation prohibitively expensive or logistically difficult. Secondly, anthropogenic fertilisation may cause outcomes misaligned from the purposes of the reserve; for example, by changing fundamental ecosystem dynamics, resulting in the loss of endemic

species and biodiversity (Isbell et al., 2013). It is possible, however, that anthropogenic impacts on natural nutrient fertilisation pathways, such as atmospheric deposition (Mahowald et al., 2008), may subsidise animal nutrient losses in some places.

In this paper, we assess how the net export of vertebrates from a fenced wildlife reserve in the southern Kalahari compares to other fluxes of P and Ca within the reserve. Removal of large vertebrates from wildlife reserves is common across southern Africa and indeed the world, most often in predator-free systems where issues of overstocking and resultant ecological degradation is a primary management concern (Gordon et al., 2004; Bothma and Du Toit, 2010). Many nutrients stored in the bodies of these removed animals are critical to the functioning of terrestrial ecosystems (Schlesinger and Bernhardt, 2013). In vertebrate species, ~80% of P and ~99% of Ca is used in the bone matrix (Suttle, 2010). Consequently, the stock of P and Ca within individuals can be reliably estimated using the allometric relationship between body mass and skeleton mass (Prange et al., 1979). We therefore focus our current study on P and Ca only. It is important to consider P and Ca together because they are nutritionally interlinked. For example, only if both elements are present in a certain ratio range can they be integrated into bone tissue in the form of hydroxyapatite (Böswald et al., 2018). Where P or Ca deficiency occurs, the growth and reproduction of plant and animal populations is severely impaired (Suttle, 2010). The southern Kalahari is notably deficient in P (Buckley et al., 1987), which means that additional losses through wildlife removal could be an important biogeochemical and conservation issue.

In an attempt to evaluate how vulnerable resident herbivores may be to management-driven nutrient export, we then assess faecal measurements from herbivores within the reserve as an indicator of forage quality and herbivore nutritional stress. Faecal analysis has been considered as a practical, non-invasive method to measure nutrient stress for large vertebrate herbivores in southern Africa as it reflects the resources actually utilised and is closely related to intake (Wrench et al., 1997; Böswald et al., 2018). As a result, it could provide a feasible method for monitoring where wildlife managers should be particularly cautious about the biogeochemical impacts of prolonged off-site removal of vertebrate individuals from wildlife areas.

Finally, we examine the role of apex predators for large-vertebrate population regulation in the context of mitigating the need for off-site removal of animals. Not only would this facilitate the retention of important nutrients within the reserve, but it is well established that local nutrient enrichment around the sites of large-vertebrate carcasses is important for maintaining ecosystem

heterogeneity and biodiversity (Carter et al., 2007). For example, Bump et al. (2009) demonstrate that elevated soil and foliar nitrogen, phosphorus and potassium leaching from ungulate carcasses created localised nutrient disturbance pulses in a northern hardwood forest, USA. Collectively, our study thus aims to quantify the loss of nutrients due to anthropogenic off-site wildlife removal, assess if resident animals are vulnerable to exacerbated nutrient stress as a result of this management strategy and explore if natural predation may be a viable alternative for herbivore regulation but without the associated loss of nutrients.

2. MATERIALS AND METHODS

2.1 Study site

Tswalu Kalahari Reserve (TKR) is a 121,700 ha fenced wildlife reserve located at S 27°13'30" and E 22°28'40" in the southern Kalahari Desert, South Africa. Prior to 1995, TKR was divided into 40 domestic livestock farms but was converted to a single wildlife reserve by the removal of internal fences and associated infrastructure. The substrate of the reserve is primarily aeolian sands of the Gordonia formation, with the emerging Korannaberg mountains formed of subgraywacke, quartzite, slate, dolomite, jasper and conglomerate (figure 1; Van Rooyen and Van Rooyen, 2017). The southern Kalahari sands are deficient in nutrients critical for animal health (Buckley et al., 1987; O'Halloran et al., 2010), which is reflected in forage deficient in important nutrients including nitrogen, phosphorus, calcium, sodium, copper and zinc (Cromhout, 2007). As a result, the wildlife managers at Tswalu Kalahari Reserve annually provide mineral licks in the form of 25kg blocks evenly distributed across the reserve to supplement wildlife diet.

TKR is split into two adjacent sections separated by a fence, which restricts animal movement; the Korannaberg section (101,700 ha) and the Lekgaba section (20,000 ha) (figure 1). Both sections include a complement of large herbivorous vertebrates native to the southern Kalahari Desert as well as a number of species that would historically have occurred seasonally (Van Rooyen and Van Rooyen, 2017) yet are now resident within the fenced system. However, the two sections support different compositions and densities of large carnivore populations. The Korannaberg section harbours cheetah (*Acinonyx jubatus*; N ~ 10) and wild dog (*Lycaon pictus*; N ~ 14), whilst the Lekgaba section harbours two prides of lion (*Panthera leo*; N ~ 24). Leopard (*Panthera pardus*), brown hyaena (*Parahyaena brunnea*) and black-backed jackal (*Canis mesomelas*) are found in both sections although population densities are unknown. It should be noted that due to the anthropogenic provision of available surface

water, predator densities can occur in TKR at higher values than expected for the xeric southern Kalahari (Roxburgh, 2010).

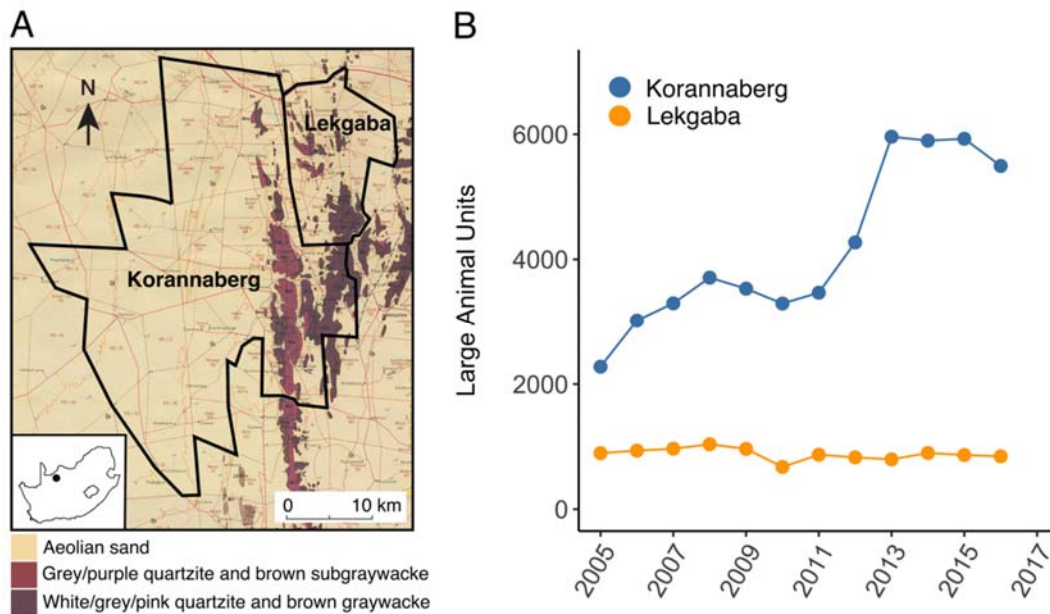


Figure 1. A) Location of Tswalu Kalahari Reserve (TKR) and major management areas (Korannaberg and Lekgaba). Underlying geology map modified from Van Rooyen and Van Rooyen (2017). Large carnivore density is low in Korannaberg and high in Lekgaba. B) Large animal units for the two management areas within TKR for the period 2005-2016. Large animal units represent a standard metric for calculating commercial stocking densities and were estimated from annual aerial count data and large animal units for herbivores after Van Rooyen (2010). Annual aerial counts were performed in March shortly prior to herbivore capture and removal which is conducted in May.

Partly driven by the different regimes of top-down regulation by carnivore populations, the dynamics of herbivore stocking densities are different in the two sections of TKR (Tokura et al., 2018). Continuous overgrazing and a pervasive drought in the southern Kalahari have led to declining veld condition in the Korannaberg section (Van Rooyen and Van Rooyen, 2017; Tokura et al., 2018). Between 1999 – 2017, the mean veld condition index in the Korannaberg section fell from 70% to 26%, where < 40% represents low grass cover with many unpalatable annual grasses and forbs (Van Rooyen and Van Rooyen, 2017). Accordingly, over the last decade TKR management has, on an annual basis, permanently exported a subset of large mammal vertebrates offsite from the Korannaberg section to maintain veld condition. Between 2009-2018, 996 (sd = 328) large vertebrates, primarily consisting of adult animals, were annually exported from the Korannaberg section and sold to other reserves. This represents an annual removal of ~10% of the total number of herbivores >10 kg in the Korannaberg section (estimated using aerial count data across the reserve between 2012-2017). This

management practice has largely been an effective method to prevent further ecological degradation as measured by the veld condition index, a measure that assesses species composition and sward structure (Van Rooyen and Van Rooyen, 2017). However, we postulate here that the short-term positive effects of animal removal may have long-term negative consequences for the ecosystem due to concomitant nutrient loss. The veld condition of the Lekgaba section where apex predators occur at higher densities has been stable and no animals were removed during the period 2009-2018 (figure 1b).

2.2 Natural and anthropogenic nutrient fluxes of TKR

Natural abiotic inputs of P and Ca to the southern Kalahari include wet and dry atmospheric deposition, rock weathering and fluvial deposition (Schlesinger and Bernhardt, 2013). In natural systems, the input of these nutrients over timescales of 10-100s of years is roughly balanced by losses from drainage and leaching, surface runoff and wind erosion (Zhou et al., 2017). Natural biotic inputs and losses are considered negligible for TKR due to the presence of fences restricting the movement of large vertebrates into and out of the reserve (Jakes et al., 2018). Consequently, changes to the nutrient mass balance of TKR arises from anthropogenic activities (Brodie and McIntyre, 2019). We calculated annual anthropogenic nutrient fluxes for P and Ca in the Korannaberg section only as no animals were removed from the Lekgaba section. The P and Ca mass balance can thus be written as:

$$\text{Nutrient mass balance} = ML - OWR \quad (\text{equation 1})$$

Where ML is nutrient input via mineral licks and OWR is nutrient loss via off-site wildlife removal. Over the period 2009-2018, the wildlife managers at TKR annually provided $17,386 \pm 1,933$ kg of phosphate mineral lick to the Korannaberg section at 17 sites distributed near permanent water sources. Each mineral lick has a mean concentration of 60g kg^{-1} of P and 120g kg^{-1} of Ca (<https://safarifeeds.co.za/products>; accessed September 2020). Annual mineral lick input of P and Ca was thus calculated using equation 2:

$$ML = M_{ml} \cdot C_{ml} \quad (\text{equation 2})$$

Where M_{ml} is the mass of mineral lick and C_{ml} is the nutrient concentration of the mineral lick. Uncertainty was calculated using the maximum and minimum estimates of M_{ml} distributed across the Korannaberg section. Approximately 80% of P and 99% of the total mass of Ca is stored within an

animal's skeleton (Suttle, 2010). Therefore, to calculate nutrient loss via off-site wildlife removal (OWR), we followed the method of Brodie and McIntyre (2019) and utilised the allometric relationship between live body mass and dry skeleton mass of $M^{1.09}$ (Prange et al., 1979):

$$OWR = \sum_{i=1}^n (0.061 \cdot M_s^{1.09} \cdot C_b) \quad (\text{equation 3})$$

Where n is the total number of animals removed off-site, M_s is the average body mass of species (s) in kg as recorded in Hempson et al. (2015) and C_b is the mean dry bone concentration of 12.30% P and 26.58% Ca recorded from the National Institute of Standards and Technology bone meal standard (https://www-s.nist.gov/srmors/view_detail.cfm?srm=1486; accessed September 2020). Uncertainty was calculated using a 15% error in skeleton mass (the standard error reported by Prange et al. (1979)) and the standard deviation in bone nutrient concentration from the National Institute of Standards and Technology bone meal standard.

2.3 Index of herbivore nutrient stress in TKR

To understand if the off-site removal of wildlife may be an important biogeochemical and conservation issue for the Korannaberg section of TKR, we examined nutrient stress in resident herbivorous mammals. Many studies have considered a critical faecal P concentration of 2000 mg kg⁻¹, below which mammal herbivore species have been documented suffering growth and reproductive issues (Wrench et al., 1997). This threshold has been used to assess the nutritional status of a number of large savannah herbivores in southern Africa including buffalo, zebra, giraffe, springbok, roan, kudu and elephant (Ullrey et al., 1997; Dorgeloh et al., 1998; Grant et al., 2000; Stapelberg et al., 2008; Pretorius et al., 2012). Calcium, however, is excreted variably in faeces and urine, so no equivalent threshold is available (Böswald et al., 2018), and thus we only consider faecal P.

Faecal samples ($n=94$) were collected from 11 herbivore species during the dry season (between April-June) in 2017 and 2019 from the Korannaberg section of TKR. This period was selected as nutrient stress for P is most severe during the dry season (Grant et al., 2000). All samples were collected fresh and frozen within 8 hours at -20°C. Samples were transported to the Endocrine Research Laboratory, University of Pretoria, for lyophilisation at -54°C and ~0.96 mbar for 5-7 days until completely dry. Dry faecal samples were subsequently pulverised using a pestle and mortar to homogenise. At the University of Pretoria Soil Sciences Laboratory, 0.25-0.30g of dried faecal powder was digested in 10ml

of Suprapur Nitric acid (65%) and analysed for P concentration using a SPECRO GENESIS Inductively coupled plasma optical emission spectrometer (ICP-OES).

2.4 Estimating nutrient retention by apex predators

Apex predators have been shown to exert a top-down control on herbivore population size (Ripple et al., 2014; le Roux et al., 2019). Where this occurs, OWR management strategies can be reduced or stopped entirely, thereby mitigating nutrient loss. At TKR, the high density and prey selection of lions (0.12 individuals km⁻²) in the Lekgaba section has been suggested to regulate herbivore populations (Tokura et al., 2018) and improve veld condition (Van Rooyen and Van Rooyen, 2017). As a result, TKR management did not deem it necessary to remove any large vertebrates from this section over the last decade. In comparison, the low density of cheetah (0.009 individuals km⁻²) and wild dog (0.014 individuals km⁻²), which favour smaller prey, have not adequately regulated herbivore populations in the Korannaberg section (figure 1b) necessitating off-site removal of animals as a management strategy. Accordingly, we compared the role that lions play in regulating herbivore populations within Lekgaba to anthropogenic regulation of herbivores in Korannaberg to understand whether natural predation by an apex carnivore can achieve similar herbivore population control, but without the associated loss of nutrients.

To do this, we utilised the lion kill modelling framework of Hayward et al. (2007). This approach uses the Jacob's prey preference index (-1 to 1; Jacobs, 1974) to assign a proportion of total lion kills to each prey species and has been validated across a productivity gradient (Hayward et al., 2007):

$$R_i = \frac{D_i p_i + p_i}{1 - D_i + 2D_i p_i} \cdot \sum K \quad (\text{equation 4})$$

Where R_i is the predicted number of kills of prey species i when there is a total of $\sum K$ observed kills. D_i represent the Jacobs' index value of species i calculated by Hayward and Kerley (2005) and p_i is the proportional abundance of prey species i . The annual number of prey animals killed (K) was estimated assuming each of the two lion prides in Lekgaba killed one large vertebrate every 5 days (Dylan Smith, Director of Research at TKR, personal communication). We calculated the proportional prey composition in Lekgaba using aerial survey data collected between 2012-2017 (SI table 2). Using the predicted number of each prey species killed (R), we could estimate the total skeleton mass recycled within Lekgaba due to lion kills using body mass estimates from Hempson et al. (2015) and the allometric scaling equation of Prange et al. (1979).

3. RESULTS

3.1 Anthropogenic nutrient fluxes in Korannaberg

During the period 2009-2018, the mean annual live animal biomass removed from the Korannaberg section of TKR was $230 \text{ kg km}^{-2} \text{ yr}^{-1}$ (table 1). This largely comprised springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), blue wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus*), greater kudu (*Tragelaphus strepsiceros*) and common eland (*Tragelaphus oryx*). The greatest number of animals removed from Korannaberg was in the 200-300 kg mass bin (68%; figure 2a). However, vertebrates >300 kg (here almost exclusively eland), which represented just 14% of individuals removed, contributed 31% to the removal of skeleton biomass. This highlights the disproportionate importance of large vertebrates for P and Ca loss out of the reserve (figure 2b). The management decision to capture and remove large vertebrates off-site was greatest during years of low antecedent precipitation, calculated as mean precipitation in Korannaberg over the preceding three years (figure 2c). Consequently, nutrient loss was highest in years with low antecedent precipitation.

Table 1. Annual anthropogenic fluxes of P and Ca into and out of Tswalu Kalahari Reserve during the period 2009 – 2018. Values in brackets represent lower and upper uncertainty estimates. Uncertainty was calculated using a 15% error in skeleton mass and the standard deviation in bone nutrient concentration from the National Institute of Standards and Technology bone meal standard (https://www-s.nist.gov/srmors/view_detail.cfm?srm=1486; accessed September 2020).

Year	Live animal biomass removed (kg km ⁻²)	Dry skeleton biomass removed (kg km ⁻²)	P export (kg km ⁻²)	Mineral lick P input (kg km ⁻²)	Difference (kg km ⁻²)	Ca Export (kg km ⁻²)	Mineral lick Ca input (kg km ⁻²)	Difference (kg km ⁻²)
2009	245.7 (208.9, 282.7)	24.4 (20.8, 28.1)	3.0 (2.5, 3.5)	1.0 (0.9, 1.1)	-2.0 (-2.6, -1.4)	6.5 (5.5, 7.5)	2.1 (1.8, 2.3)	-4.4 (-5.7, -3.2)
2010	170.8 (145.2, 196.4)	16.8 (14.3, 19.4)	2.1 (1.7, 2.4)	1.0 (0.9, 1.1)	-1.1 (-1.5, -0.6)	4.5 (3.8, 5.2)	2.1 (1.8, 2.3)	-2.4 (-3.4, -1.5)
2011	151.3 (128.6, 174.0)	15.0 (12.7, 17.2)	1.8 (1.5, 2.2)	1.0 (0.9, 1.1)	-0.8 (-1.3, -0.4)	4.0 (3.4, 4.6)	2.1 (1.8, 2.3)	-1.9 (-2.8, -1.1)
2012	129.2 (109.8, 148.6)	12.9 (10.9, 14.8)	1.6 (1.3, 1.8)	1.0 (0.9, 1.1)	-0.6 (-0.9, -0.2)	3.4 (2.9, 4.0)	2.1 (1.8, 2.3)	-1.3 (-2.2, -0.6)
2013	158.7 (134.9, 182.5)	15.9 (13.5, 18.3)	2.0 (1.6, 2.3)	1.0 (0.9, 1.1)	-1.0 (-1.4, -0.5)	4.2 (3.6, 4.9)	2.1 (1.8, 2.3)	-2.1 (-3.1, -1.3)
2014	190.7 (162.1, 219.3)	19.2 (16.3, 22.1)	2.4 (2.0, 2.8)	1.0 (0.9, 1.1)	-1.4 (-1.9, -0.9)	5.1 (4.3, 5.9)	2.1 (1.8, 2.3)	-3.0 (-4.1, -2.0)
2015	202.0 (171.7, 232.3)	20.4 (17.3, 23.4)	2.5 (2.1, 2.9)	1.0 (0.9, 1.1)	-1.5 (-2.0, -1.0)	5.4 (4.6, 6.3)	2.1 (1.8, 2.3)	-3.3 (-4.5, -2.3)
2016	394.1 (335.0, 453.2)	40.2 (34.2, 46.3)	4.9 (4.1, 5.8)	1.0 (0.9, 1.1)	-3.9 (-4.9, -3.0)	10.7 (9.0, 12.4)	2.1 (1.8, 2.3)	-8.6 (-10.6, -6.7)
2017	194.9 (165.7, 224.1)	19.7 (16.8, 22.7)	2.4 (2.0, 2.8)	1.0 (0.9, 1.1)	-1.4 (-1.9, -0.9)	5.2 (4.4, 6.1)	2.1 (1.8, 2.3)	-3.1 (-4.3, -2.1)
2018	457.7 (389.1, 526.4)	47.2 (40.2, 54.3)	5.8 (4.9, 6.8)	1.0 (0.9, 1.1)	-4.8 (-5.9, -3.8)	12.6 (10.6, 14.6)	2.1 (1.8, 2.3)	-10.5 (-12.8, -8.3)
Decade Total	2295.2 (1950.9, 2639.5)	231.8 (197.0, 266.6)	28.5 (23.7, 33.3)	10.0 (9.0, 11.0)	-18.5 (-24.3, -12.7)	61.6 (52.1, 71.5)	21.0 (18.0, 23.0)	-40.6 (-53.5, -29.1)

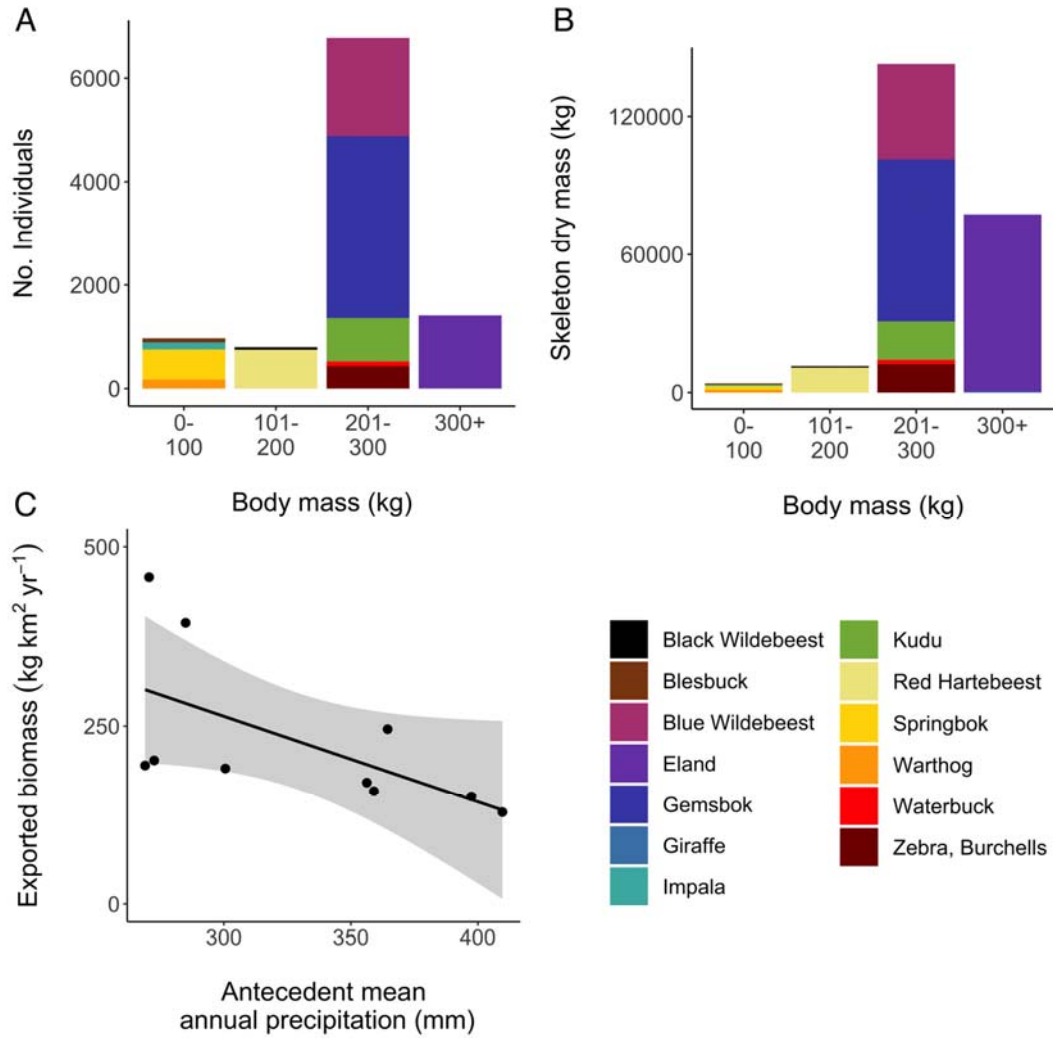


Figure 2. A) The total number of herbivores and B) dry mass of skeleton removed from the Korannaberg section of Tswalu Kalahari Reserve during the period 2009-2018 summarised into bins based on the body mass (kg) of each species. C) Relationship between antecedent precipitation for Korannaberg and exported animal biomass for the period 2009-2018. Antecedent precipitation for each point of annually exported herbivore biomass was calculated as the mean annual precipitation from 20 rain gauges distributed across Korannaberg over the preceding three years.

Mean loss of P and Ca via wildlife removal was 2.9 and 6.2 kg km⁻² yr⁻¹. This compares to 1.0 and 2.1 kg km⁻² yr⁻¹ of P and Ca added via the provision of mineral licks (table 1). In every year between 2009-2018, the off-site removal of wildlife resulted in a net deficit for P and Ca for TKR (figure 3). If it is assumed that natural fluxes of these elements are in steady state, then anthropogenic activities have resulted in a total net deficit of 18.5 kg km⁻² of P and 40.6 kg km⁻² of Ca over the decade (table 1).

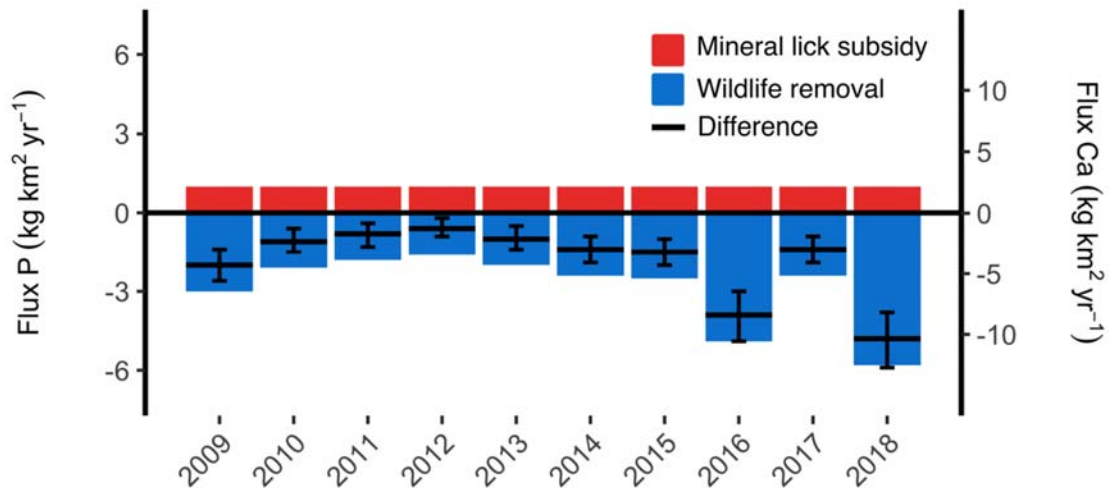


Figure 3. Annual fluxes of P and Ca provided by mineral lick subsidy and off-site removal of wildlife in Tswalu Kalahari Reserve over the period 2009 – 2018. Error bars represent uncertainty in the difference between these fluxes from Table 1.

3.2 Herbivore nutrient stress in Korannaberg

In the Korannaberg section of TKR, 22% of individuals are below the faecal P threshold of 2000 mg kg⁻¹ (figure 4). In general, faecal P concentration was found to decrease with body mass, whilst there was no consistent difference between hindgut and ruminant gut fermentation strategies. This indicates that with respect to P, Korannaberg is a low-nutrient environment and long-term, continued removal of wildlife may cause further nutritional stress.

3.3 Top-down control of herbivores in Lekgaba

In total, the two lion prides in Lekgaba (n~24) are estimated to kill 193 large vertebrates annually. This primarily constitutes gemsbok (*Oryx gazelle*, 97), Burchell's zebra (*Equus quagga*, 25) and blue wildebeest (*Connochaetes taurinus*, 22) (SI table 2). The annual biomass of all prey animals killed by lions in Lekgaba scaled by area is 224 kg km⁻² yr⁻¹. This value is close to the mean annual animal biomass scaled by area removed via OWR in the Korannaberg section (230 kg km⁻² yr⁻¹) indicating that natural predation is capable of achieving similar herbivore population control as management removals, but without the associated loss of nutrients.

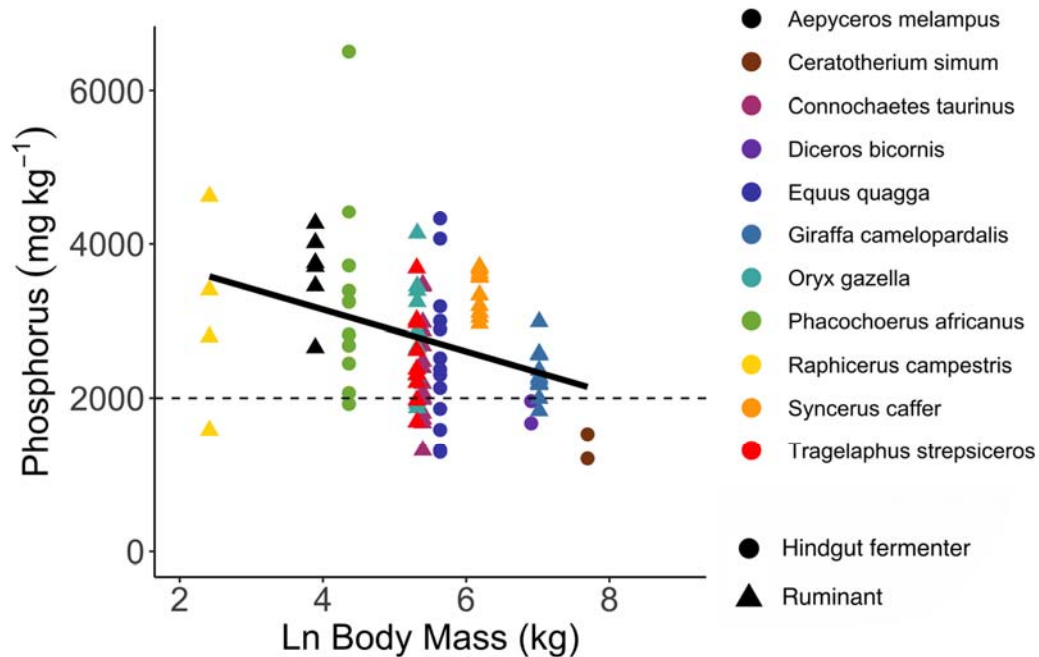


Figure 4. Faecal phosphorus (P) in relation to the natural log of herbivore body size (in kilograms) for 11 herbivore species in the Korannaberg section of Tswalu Kalahari Reserve (TKR). The trendline represents a generalised-least squares model fit for all herbivores. The dashed line represents a widely cited minimum threshold of 2000 mg kg⁻¹ (Wrench et al., 1997), below which most vertebrate begin suffering growth and reproductive issues. Note that faecal collection was collected in the early dry season (April-June).

4. DISCUSSION

4.1 Off-site wildlife removal (OWR)

Nutrients concentrated within an animal may “escape” from a landscape if a) an animal migrates under its own free will, b) it is killed and removed for meat or c) it is selectively removed for conservation reasons. We have shown in this study that the loss of nutrients via OWR for conservation reasons is of a similar magnitude to nutrient loss from migration and hunting (Flueck, 2009; Brodie and McIntyre, 2019). Indeed, compared to hunting-induced mineral loss in two nearby Botswanan sites estimated by Brodie and McIntyre (2019), P and Ca loss from TKR is 29-290 times larger. In relation to the present-day atmospheric deposition flux of P modelled by Mahowald et al. (2008), annual off-site wildlife removal is of an equivalent magnitude (1-5 kg km⁻² yr⁻¹), despite an increase in P deposition in the southern Kalahari over the last century due to industrial activities and biomass burning. Further, because rock weathering inputs of P at TKR are small (Buckley et al., 1987), in years when the annual removal of herbivores from TKR is high (>300 kg live animal biomass km⁻² yr⁻¹) the loss of P from OWR

may be larger than the combined total input from atmospheric deposition, rock weathering and anthropogenic mineral licks. Given that OWR in Korannaberg is negatively related to antecedent precipitation (figure 2c), this indicates that increasingly variable rainfall regimes across southern Africa as a result of climate change (Yu et al., 2017; Tokura et al., 2018) may play a role in exacerbating nutrient losses from the Korannaberg section of TKR as the need for OWR increases.

The estimates provided in our study are a first approximation of nutrient loss due to large vertebrate removal from wildlife reserves and can be improved with future research. In particular, we do not include non-skeletal reserves of P and Ca and rely upon the allometric scaling of dry skeleton mass by Prange et al. (1979), which is based on a small number of observations. We discuss our confidence in this relationship and the need for future research on this topic in SI text 1.

4.2 Increased nutrient stress due to OWR

Imbalance between nutrient inputs and losses has been shown to impact the stability of ecosystems throughout the world (Schlesinger and Bernhardt, 2013). In the Kalahari Desert, decreasing soil fertility measured along the Kalahari Transect (KT) from Zambia to South Africa is associated with decreasing soil microbial activity, plant production and foliar nutrient concentrations (O'Halloran et al., 2010). This suggests that additional loss of nutrient fertility due to OWR may impact the ecological stability of Korannaberg as a result of feedbacks between soils, plants and animals. This is particularly pertinent for TKR given that a number of large herbivore individuals in the Korannaberg section of TKR may already be suffering seasonal or chronic nutrient shortage (figure 4). The faecal samples used here were collected in the early dry season, suggesting that individuals that were under the critical faecal P threshold of 2000 mg kg⁻¹ may remain under for the full length of the dry season (Grant et al., 2000). In a study looking at the condition of buffalo in the Korannaberg section of TKR, Cromhout (2007) found that faecal samples collected in the late dry season (September) had much lower faecal P when compared to the faecal samples included in this study. In particular, lactating females (1740 mg kg⁻¹) and adult bulls (1630 mg kg⁻¹) had low P concentrations, suggesting particularly high P requirement (lactation) or low forage capability (reduced home range) for these groups. It has also been suggested that P requirement may scale with body mass (le Roux et al., 2020). The postulated reason for this is due to P requirements scaling with the positive skeleton allometry from Prange et al. (1979). Our faecal P concentration results support previous studies for the allometric relationship between body mass and faecal P concentration (figure 4); however, we also suggest diet quality as an alternative possible explanation for this relationship (see SI text 2 for details). In this case, individuals

that are lactating, defending territories, pursuing sexual partners or investing in large amounts of skeleton growth will be most susceptible to nutrient stress and the possible biogeochemical impacts of off-site wildlife removal.

Consequently, whilst off-site wildlife removal may mitigate ecological degradation due to overstocking in the short-term (Van Rooyen and Van Rooyen, 2017), the additive loss of P, Ca and other important nutrients annually exported in the bodies of large-vertebrates may cause separate issues related to declining ecosystem fertility and associated feedbacks in the long-term.

4.3 Role of predators and bone scavengers

We estimate that the biomass of large vertebrates killed by lions in Lekgaba compares closely to the flux annually removed via OWR from the Korannaberg section of TKR. Consequently, we demonstrate in a site directly adjacent to Korannaberg that natural predation levels can reduce herbivore populations sufficiently and mitigate the need for OWR. From a nutrient perspective, however, the key difference between these two processes is that lion kills ensure that nutrients concentrated in the bodies of prey animals are recycled within the reserve.

Following a lion kill, bone scavengers in TKR such as brown hyaena (*Parahyaena brunnea*) break down the carcass skeleton. Splinters of bone from this process have been shown to provide an important source of P and Ca for birds in other nutrient-poor areas of South Africa (Richardson et al., 1986). Furthermore, hyaenas create P and Ca rich faecal deposits (Kruunk, 1972), which we posit, may help redistribute these minerals across the landscape. As bone scavengers often have large home ranges and opportunistically transverse fence boundaries, it is possible that some of the nutrients from lion carcasses are lost from the reserve. However, Williams et al. (2021) showed that in reserves where fence integrity is high, scavengers such as brown hyaena generally remain within the reserve due to the abundance of sympatric predators and high levels of carrion, so the loss of nutrients via this vector is assumed negligible.

Predators have been shown to influence nutrient dynamics via a number of direct (e.g. defecation) and indirect (e.g. herbivore movement) pathways (reviewed in Schmitz et al., 2010). Here, we show that in closed, fenced wildlife reserves, an absence of apex predators in densities high enough to regulate herbivore populations, generates an additional vector of nutrient leakage from wildlife reserves through unchecked herbivore population growth and the necessity of anthropogenic off-site animal removal. Within the context of predicted increasingly variable rainfall regimes over the

southern Kalahari (Yu et al., 2017), the reintroduction of additional apex predators in the Korannaberg section of TKR could help buffer ecosystems against further nutrient loss over coming decades.

4.4 Applications for wildlife reserves globally

TKR is not in a unique situation with respect to either the magnitude of animals annually exported from the reserve or being located in a nutrient-poor environment. Many terrestrial wildlife reserves throughout the world are located on marginal land where agriculture is not economically feasible (Joppa and Pfaff, 2009). Accordingly, the results presented here are applicable for wildlife managers working in low-nutrient environments across the world. In some places, OWR may be a continuation of a process that has a long history. For example, the present-day culling and removal of red deer (*Cervus elaphus*) in Scottish uplands to prevent overgrazing may continue a centuries-old nutrient-removal process from landscapes already depleted in key nutrients due to thin soils, high rainfall and extensive sheep grazing (Sansom, 1999). Where large carnivores have been extirpated or the effects of climate change are severe, herbivore overstocking necessitates the removal of large numbers of animals. Wildlife managers should monitor nutrient concentrations in soils, plants and faeces to ensure that management practices do not have unintended biogeochemical consequences and, where possible, holistic strategies that promote the retention of nutrients within the reserve - such as the reintroduction of large carnivores - should be preferred.

Authors' Contributions

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

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Data Availability Statement

Data available via the Figshare Repository:

https://figshare.com/articles/dataset/Abraham_2021_Tswalu_faecal_dataset/14167133 (Abraham et al., 2021)

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