DOI: 10.1111/1365-2664.13878

# **RESEARCH ARTICLE**

# Large predators can mitigate nutrient losses associated with off-site removal of animals from a wildlife reserve

Andrew J. Abraham<sup>1,2</sup> | Andrea B. Webster<sup>3</sup> | Tomos O. Prys-Jones<sup>1</sup> | | Elizabeth le Roux<sup>2,4</sup> | Dylan Smith<sup>5</sup> | Duncan McFayden<sup>5</sup> | Pieter C. de Jager<sup>6</sup> | | Marcus Clauss<sup>7</sup> | Christopher E. Doughty<sup>1</sup>

<sup>1</sup>School of Informatics, Computing and Cyber Systems, Northern Arizona University, Flagstaff, AZ, USA; <sup>2</sup>School of Geography and the Environment, Environmental Change Institute, University of Oxford, Oxford, UK; <sup>3</sup>Mammal Research Institute, University of Pretoria, Pretoria, South Africa; <sup>4</sup>Centre for Biodiversity Dynamics in a Changing World (BIOCHANGE), Section of Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark; <sup>5</sup>Tswalu Kalahari Reserve, Tswalu, Northern Cape, South Africa; <sup>6</sup>Department of Plant and Soil Sciences, Faculty of Natural and Agricultural Sciences, University of Pretoria, Pretoria, South Africa and <sup>7</sup>Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland

#### Correspondence

Andrew J. Abraham Email: andrew.abraham@nau.edu

#### Funding information

National Aeronautics and Space Administration, Grant/Award Number: 16- HW16\_2-0025; Google; Royal Society Newton International Fellowship

Handling Editor: Sungwon Hong

# 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 whether 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<sup>-2</sup> year<sup>-1</sup>, respectively. This compares to 1.0 and 2.1 kg km<sup>-2</sup> year<sup>-1</sup> 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<sup>2</sup> of P and 40.6 kg/km<sup>2</sup> 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 2,000 mg/kg, 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.

#### 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 (Holdø 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 (du P Bothma and du Toit, 2010; Newmark, 1993).

Although 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 McInturf et al., 2019; Subalusky & Post, 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 (Doughty et al., 2016; Roman et al., 2014).

Although 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 elea-phus* 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. First, wildlife reserves often cover vast areas making fertilisation prohibitively expensive or logistically difficult. Second, 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 is compared 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 are primary management concerns (du P Bothma and du Toit, 2010; Gordon et al., 2004). Many nutrients stored in the bodies of these removed animals are critical to the functioning of terrestrial ecosystems (Schlesinger & Bernhardt, 2013). In vertebrate species, ~80% of P and ~99% of Ca are 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 are 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 (Böswald et al., 2018; Wrench et al., 1997). 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 also 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 offsite wildlife removal (OWR), assess whether resident animals are vulnerable to exacerbated nutrient stress as a result of this management strategy and explore whether 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 & 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 & 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), whereas 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).

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



**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

the southern Kalahari have led to declining veld condition in the Korannaberg section (Van Rooyen & Van Rooyen, 2017; Tokura et al., 2018). Between 1999 and 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 & 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 and 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 and 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 & 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 & 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 arise from anthropogenic activities (Brodie & 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:

Nutrient mass balance = 
$$ML - OWR$$
, (1)

where ML is the nutrient input via mineral licks and OWR is the nutrient loss via OWR. 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<sup>-1</sup> of P and 120g kg<sup>-1</sup> of Ca (https://safarifeeds.co.za/products; accessed

September 2020). Annual mineral lick input of P and Ca was thus calculated using Equation 2:

$$ML = M_{ml}. C_{ml}, \qquad (2)$$

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 are stored within an animal's skeleton (Suttle, 2010). Therefore, to calculate nutrient loss via 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<sup>1.09</sup> (Prange et al., 1979):

OWR = 
$$\sum_{i=1}^{n} \left( 0.061. \, M_s^{1.09}. \, C_b \right),$$
 (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 whether 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 2,000 mg/kg, 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 (Dorgeloh et al., 1998; Grant et al., 2000; Pretorius et al., 2012; Stapelberg et al., 2008; Ullrey et al., 1997). 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 and 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 hr 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– 0.30 g of dried faecal powder was digested in 10 ml 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 (le Roux et al., 2019; Ripple et al., 2014). 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<sup>2</sup>) in the Lekgaba section have been suggested to regulate herbivore populations (Tokura et al., 2018) and improve veld condition (Van Rooyen & 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<sup>2</sup>) and wild dog (0.014 individuals/km<sup>2</sup>), 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):

$$R_{i} = \frac{D_{i}p_{i} + p_{i}}{1 - D_{i} + 2D_{i}p_{i}}.\sum K,$$
(4)

where  $R_i$  is the predicted number of kills of prey species *i* when there is a total of  $\Sigma K$  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 and 2017 (Table S2). 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 kg km<sup>-2</sup> year<sup>-1</sup> (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 3 years (Figure 2c). Consequently, nutrient loss was highest in years with low antecedent precipitation.

Mean loss of P and Ca via wildlife removal was 2.9 and 6.2 kg km<sup>-2</sup> year<sup>-1</sup>. This compares to 1.0 and 2.1 kg km<sup>-2</sup> year<sup>-1</sup> of P and Ca added via the provision of mineral licks (Table 1). In every year between 2009 and 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 an-thropogenic activities have resulted in a total net deficit of 18.5 kg/km<sup>2</sup> of P and 40.6 kg/km<sup>2</sup> of Ca over the decade (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 2,000 mg/kg (Figure 4). In general, faecal P concentration was found to decrease with body mass while 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 ( $n \sim 24$ ) are estimated to kill 193 large vertebrates annually. This primarily constitutes gemsbok *Oryx gazelle* (97), Burchell's zebra *Equus quagga* (25) and blue wildebeest *C. taurinus* (22; Table S2). The annual biomass of all prey

one meal	standard (https://www-s.nist	.gov/srmors/view_deta	ail.cfm?srm=1486; ac	cessed September 2	2020)			
Year	Live animal biomass removed (kg/km <sup>2</sup> )	Dry skeleton biomass removed (kg/km <sup>2</sup> )	P export (kg/km²)	Mineral lick P input (kg/km <sup>2</sup> )	Difference (kg/km²)	Ca export (kg/km <sup>2</sup> )	Mineral lick Ca input (kg/km <sup>2</sup> )	Difference (kg/km <sup>2</sup> )
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	2,295.2 (1950.9, 2,639.5)	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)

animals killed by lions in Lekgaba scaled by area is 224 kg km<sup>-2</sup> year<sup>-1</sup>. This value is close to the mean annual animal biomass scaled by area removed via OWR in the Korannaberg section (230 kg km<sup>-2</sup> year<sup>-1</sup>) indicating that natural predation is capable of achieving similar herbivore population control as management removals, but without the associated loss of nutrients.

# 4 | DISCUSSION

#### 4.1 | Off-site wildlife removal

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 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 (Brodie & McIntyre, 2019; Flueck, 2009). 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 OWR is of an equivalent magnitude (1-5 kg km<sup>-2</sup> year<sup>-1</sup>), despite an increase in P deposition in the southern Kalahari over the last century due to industrial activities and biomass burning. Furthermore, 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<sup>-2</sup> year<sup>-1</sup>) 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 (Tokura et al., 2018; Yu et al., 2017) 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 Supporting Information 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 & Bernhardt, 2013). In the Kalahari Desert, decreasing soil fertility measured along the Kalahari Transect (KT) from

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

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



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 3 years

**FIGURE 3** Annual fluxes of P and Ca provided by mineral lick subsidy and offsite 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

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 2,000 mg/kg 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 (1,740 mg/kg) and adult bulls (1,630 mg/kg) 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



**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 2,000 mg/kg (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)

between body mass and faecal P concentration (Figure 4); however, we also suggest diet quality as an alternative possible explanation for this relationship (see Supporting Information 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 OWR.

Consequently, while OWR may mitigate ecological degradation due to overstocking in the short term (Van Rooyen & 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 *P. 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 (Kruuk, 1972), which we posit, that 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 & 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.

#### ACKNOWLEDGEMENTS

A.J.A. and C.E.D. acknowledge funding by NASA award 16-HW16\_2-0025 and a Google Earth Engine research award. E.I.R. was funded through the Royal Society Newton International Fellowship. We thank the management and staff of Tswalu Kalahari Reserve and the Tswalu Foundation for their support and facilitation of this project. We also thank Paul Beier for helpful comments during the preparation of this manuscript and John Coppock, Duncan Leese and Scott Abraham for their help in collecting faecal samples. Dr Nokubonga Mgqatsa of Rhodes University kindly translated our manuscript.

### AUTHORS' CONTRIBUTIONS

A.J.A., D.S. and C.E.D. conceived the ideas and designed the methodology; A.J.A., A.B.W., T.O.P.-J. collected the faecal samples; A.J.A., T.O.P.-J., E.I.R. and M.C. analysed the data; A.J.A. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### DATA AVAILABILITY STATEMENT

Data available via the Figshare Repository https://figshare.com/ articles/dataset/Abraham\_2021\_Tswalu\_faecal\_dataset/14167133 (Abraham et al., 2021).

#### ORCID

Andrew J. Abraham https://orcid.org/0000-0001-8625-8851 Andrea B. Webster https://orcid.org/0000-0002-7136-4421 Tomos O. Prys-Jones https://orcid.org/0000-0001-6472-302X Elizabeth le Roux https://orcid.org/0000-0001-8468-8284 Pieter C. de Jager https://orcid.org/0000-0002-7361-9002 Christopher E. Doughty https://orcid.org/0000-0003-3985-7960

#### REFERENCES

- Abraham, A. J., Webster, A. B., Prys-Jones, T. O., le Roux, E., Smith, D., McFayden, D., de Jager, C., Clauss, M., & Doughty, C. E. (2021).
  Data from: Large predators can mitigate nutrient losses associated with off-site removal of animals from a wildlife reserve. *Figshare Repository.* https://figshare.com/articles/dataset/Abraham\_2021\_ Tswalu\_faecal\_dataset/14167133
- Böswald, L. F., Dobenecker, B., Clauss, M., & Kienzle, E. (2018). A comparative meta-analysis on the relationship of faecal calcium and phosphorus excretion in mammals. *Journal of Animal Physiology* and Animal Nutrition, 102(2), 370–379. https://doi.org/10.1111/ jpn.12844
- Brodie, J. F., & McIntyre, P. B. (2019). Bushmeat biogeochemistry: Hunting tropical mammals alters ecosystem phosphorus budgets. *Proceedings of the Royal Society B: Biological Sciences*, 286(1907), 20190966. https://doi.org/10.1098/rspb.2019.0966
- Buckley, R., Wasson, R., & Gubbi, A. (1987). Phosphorus and potassium status of arid dunefield soils in central Australia and southern Africa, and biogeographic. *Journal of Arid Environments*, 13, 211–216.
- Bump, J. K., Webster, C. R., Vucetich, J. A., Peterson, R. O., Shields, J. M., & Powers, M. D. (2009). Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. *Ecosystems*, 12(6), 996–1007. https://doi.org/10.1007/s10021-009-9274-0
- Carter, D. O., Yellowlees, D., & Tibbett, M. (2007). Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften*, 94(1), 12–24. https://doi.org/10.1007/s00114-006-0159-1
- Cromhout, M. (2007). The ecology of the African buffalo in the Eastern Kalahari region. University of Pretoria.
- Dorgeloh, W. G., Van Hoven, W., & Rethman, N. F. G. (1998). Faecal analysis as an indicator of the nutritional status of the diet of roan antelope in South Africa. South African Journal of Wildlife Research-24-Month Delayed Open Access, 28(1), 16–21.

- Doughty, C. E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E. S., Malhi, Y., Dunning, J. B., & Svenning, J.-C. (2016). Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences of the United States of America*, 113(4), 868–873. https://doi. org/10.1073/pnas.1502549112
- du P Bothma, J., & du Toit, J. G. (2010). *Game ranch management* (p. 979). Van Schaik Publishers.
- Flueck, W. T. (2009). Biotic translocation of phosphorus: The role of deer in protected areas. *Sustainability*, 1(2), 104–119. https://doi. org/10.3390/su1020104
- Gordon, I. J., Hester, A. J., & Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, 41(6), 1021–1031.
- Grant, C. C., Peel, M. J. S., & Van Ryssen, J. B. J. (2000). Nitrogen and phosphorus concentration in faeces: An indicator of range quality as a practical adjunct to existing range evaluation methods. *African Journal of Range and Forage Science*, 17(1–3), 81–92. https://doi. org/10.2989/10220110009485743
- Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). Journal of Zoology, 267(3), 309–322. https://doi. org/10.1017/S0952836905007508
- Hayward, M. W., O'Brien, J., Hofmeyr, M., & Kerley, G. I. H. (2007). Testing predictions of the prey of lion derived from modeled prey preferences. *The Journal of Wildlife Management*, 71(5), 1567–1575. https://doi.org/10.2193/2006-264
- Hempson, G. P., Archibald, S., & Bond, W. J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science*, 350(6264), 1056–1061.
- Holdø, R. M., Dudley, J. P., & McDowell, L. R. (2002). Geophagy in the African elephant in relation to availability of dietary sodium. *Journal* of Mammalogy, 83(3), 652-664. https://doi.org/10.1644/1545-1542(2002)083<0652:GITAEI>2.0.CO;2
- Isbell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy* of Sciences of the United States of America, 110(29), 11911–11916. https://doi.org/10.1073/pnas.1310880110
- Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia*, 14(4), 413–417. https://doi.org/10.1007/BF00384581
- Jakes, A. F., Jones, P. F., Paige, L. C., Seidler, R. G., & Huijser, M. P. (2018). A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems. *Biological Conservation*, 227, 310–318. https://doi.org/10.1016/j.biocon.2018.09.026
- Joppa, L. N., & Pfaff, A. (2009). High and far: Biases in the location of protected areas. PLoS ONE, 4(12), e8273. https://doi.org/10.1371/ journal.pone.0008273
- Kruuk, H. (1972). The spotted hyena: A study of predation and social behaviour. University of Chicago Press.
- Le Roux, E., Marneweck, D. G., Clinning, G., Druce, D. J., Kerley, G. I., & Cromsigt, J. P. (2019). Top-down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography*, 42(6), 1115–1123.
- le Roux, E., van Veenhuisen, L. S., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2020). Animal body size distribution influences the ratios of nutrients supplied to plants. Proceedings of the National Academy of Sciences of the United States of America, 117(36), 22256–22263. https://doi.org/10.1073/pnas.2003269117
- Mahowald, N., Jickells, T. D., Baker, A. R., Artaxo, P., Benitez-Nelson, C. R., Bergametti, G., Bond, T. C., Chen, Y., Cohen, D. D., Herut, B., Kubilay, N., Losno, R., Luo, C., Maenhaut, W., McGee, K. A., Okin, G. S., Siefert, R. L., & Tsukuda, S. (2008). Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Global Biogeochemical Cycles*, 22(4), GB4026. https://doi.org/10.1029/2008GB003240

- McInturf, A. G., Pollack, L., Yang, L. H., & Spiegel, O. (2019). Vectors with autonomy: What distinguishes animal-mediated nutrient transport from abiotic vectors? *Biological Reviews*, 94(5), 1761–1773. https:// doi.org/10.1111/brv.12525
- McNaughton, S. J. (1990). Mineral nutrition and seasonal movements of African migratory ungulates. *Nature*, 345(6276), 613–615.
- Newmark, W. D. (1993). The role and design of wildlife corridors with examples from Tanzania. *Ambio*, 22(8), 500–504.
- O'Halloran, L. R., Shugart, H. H., Wang, L., Caylor, K. K., Ringrose, S., & Kgope, B. (2010). Nutrient limitations on aboveground grass production in four savanna types along the Kalahari Transect. *Journal* of Arid Environments, 74(2), 284–290. https://doi.org/10.1016/j.jarid env.2009.08.012
- Prange, H. D., Anderson, J. F., & Rahn, H. (1979). Scaling of skeletal mass to body mass in birds and mammals. *The American Naturalist*, 113(1), 103–122. https://doi.org/10.1086/283367
- Pretorius, Y., Stigter, J. D., de Boer, W. F., van Wieren, S. E., de Jong, C. B., de Knegt, H. J., Grant, C. C., Heitkönig, I., Knox, N., Kohi, E., Mwakiwa, E., Peel, M. J. S., Skidmore, A. K., Slotow, R., van der Waal, C., van Langevelde, F., & Prins, H. H. T. (2012). Diet selection of African elephant over time shows changing optimization currency. *Oikos*, 121(12), 2110–2120. https://doi.org/10.1111/ j.1600-0706.2012.19680.x
- Richardson, P. R. K., Mundy, P. J., & Plug, I. (1986). Bone crushing carnivores and their significance to osteodystrophy in griffon vulture chicks. *Journal of Zoology*, 210(1), 23–43. https://doi.org/10.1111/ j.1469-7998.1986.tb03618.x
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343(6167). https://doi.org/10.1126/science. 1241484
- Roman, J., Estes, J. A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J. B., Nicol, S., Pershing, A., & Smetacek, V. (2014). Whales as marine ecosystem engineers. *Frontiers in Ecology and the Environment*, 12(7), 377–385. https://doi.org/10.1890/130220
- Rothman, J. M., Van Soest, P. J., & Pell, A. N. (2006). Decaying wood is a sodium source for mountain gorillas. *Biology Letters*, 2(3), 321–324. https://doi.org/10.1098/rsbl.2006.0480
- Roxburgh, D. J. (2010). Prey and range use of lions on Tswalu Kalahari Reserve. University of Pretoria.
- Sansom, A. L. (1999). Upland vegetation management: The impacts of overstocking. Water Science and Technology, 39(12), 85–92. https:// doi.org/10.2166/wst.1999.0533
- Schlesinger, W. H., & Bernhardt, E. S. (2013). Biogeochemistry: An analysis of global change. Academic Press.
- Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology letters*, 13(10), 1199–1209.
- Sillanpää, M. (1982). Micronutrients and the nutrient status of soils: A global study (Vol. 48). Food & Agriculture Organization.
- Stapelberg, F. H., Van Rooyen, M. W., du Bothma, J. D. P. (2008). Spatial and temporal variation in nitrogen and phosphorus concentrations

in faeces from springbok in the Kalahari. African Journal of Wildlife Research, 38(1), 82–87. https://doi.org/10.3957/0379-4369-38.1.82

Subalusky, A. L., & Post, D. M. (2019). Context dependency of animal resource subsidies. *Biological Reviews*, 94(2), 517–538. https://doi. org/10.1111/brv.12465

Suttle, N. F. (2010). Mineral nutrition of livestock. Cabi.

- Thornton, I. (2002). Geochemistry and the mineral nutrition of agricultural livestock and wildlife. *Applied Geochemistry*, 17(8), 1017–1028. https://doi.org/10.1016/S0883-2927(02)00079-3
- Tokura, W., Jack, S. L., Anderson, T., & Hoffman, M. T. (2018). Long-term variability in vegetation productivity in relation to rainfall, herbivory and fire in Tswalu Kalahari Reserve. *Koedoe*, 60(1), 1–18. https://doi. org/10.4102/koedoe.v60i1.1473
- Ullrey, D. E., Crissey, S. D., & Hintz, H. F. (1997). *Elephants: Nutrition and dietary husbandry*. Nutrition Advisory Group East Lansing.
- van Rooyen, N. (2010). Veld management in the African savannas under current climatic conditions: Ecological and economic wildlife stocking rates. In J. du P. Bothma & J. G. du Toit, (Ed.), *Game ranch management* (5th ed., pp. 801–815). Van Schaik Publishers.
- van Rooyen, N., & van Rooyen, G. (2017). Ecological Evaluation of Tswalu Kalahari Reserve.
- Williams, K. S., Williams, S. T., Welch, R. J., Marneweck, C. J., Mann, G. K.
  H., Pitman, R. T., Whittington-Jones, G., Balme, G. A., Parker, D. M., & Hill, R. A. (2021). Assumptions about fence permeability influence density estimates for brown hyaenas across South Africa. *Scientific Reports*, 11, 620. https://doi.org/10.1038/s41598-020-77188-7
- Wrench, J. M., Meissner, H. H., & Grant, C. C. (1997). Assessing diet quality of African ungulates from faecal analyses: The effect of forage quality, intake and herbivore species. *Koedoe*, 40(1), 125–136. https://doi.org/10.4102/koedoe.v40i1.268
- Yu, K., Saha, M. V., & D'Odorico, P. (2017). The effects of interannual rainfall variability on tree-grass composition along Kalahari rainfall gradient. *Ecosystems*, 20(5), 975–988. https://doi.org/10.1007/s1002 1-016-0086-8
- Zhou, Q., Daryanto, S., Xin, Z., Liu, Z., Liu, M., Cui, X., & Wang, L. (2017). Soil phosphorus budget in global grasslands and implications for management. *Journal of Arid Environments*, 144, 224–235. https://doi. org/10.1016/j.jaridenv.2017.04.008

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Abraham AJ, Webster AB, Prys-Jones TO, et al. Large predators can mitigate nutrient losses associated with off-site removal of animals from a wildlife reserve. *J Appl Ecol.* 2021;58:1360–1369. <u>https://doi.</u> org/10.1111/1365-2664.13878