








RESEARCH ARTICLE

Predators and management influence adult sex ratio of ungulate communities: Synergies and challenges for contemporary conservation

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Handling Editor: Abishek Harihar**Abstract**

1. Adult sex ratio (ASR) is important for the ecology, behaviour and life histories of large ungulate populations. ASR, however, varies considerably in wild populations, with driving factors not fully understood. Predation is one possible driver and can alter the ASR of prey species via direct and indirect mechanisms. In the absence of predators, management may also alter ungulate ASR via sex-biased animal removal.
2. Here, we utilised a wildlife reserve divided into two sections, but with comparable environments and ungulate communities. One section hosts lions (*Panthera leo*) with no management-driven wildlife offtakes, while the other has cheetah (*Acinonyx jubatus*), wild dogs (*Lycaon pictus*) and management periodically removes ungulates. To assess the impacts of these differences on ungulate ASR, we surveyed 12 ungulate species (body mass: 10–2000 kg) that co-occur in both sections, revealing that five ungulate species exhibited statistically significant differences in ASR between sections.
3. Predators exerted contrasting direct effects on prey ASR: lion generally displayed a bias towards killing male prey individuals, cheetah had a weak female bias in smaller prey species, and wild dog displayed no general pattern across species. A meta-analysis of sex-biased predator mortality in 53 ungulate populations across Africa broadly supported our findings. Lion appeared to further elicit indirect changes to herding and sexual segregation behaviours in larger-bodied ungulate species, but we found limited evidence for changes in ungulate nutrition or body condition.

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4. In the section without lions, wildlife management annually removed ~10%–20% of larger-bodied ungulate populations, with a mild bias towards male individuals. This intervention somewhat replicated the direct effects of natural lion predation on ungulate ASR. Management removals did not, however, stimulate the same behavioural effects in ungulate populations as lions.
5. *Synthesis and applications.* Predators and management can influence ungulate adult sex ratio (ASR) through multiple pathways, with important implications for breeding system evolution and population dynamics. Given many landscapes are defaunated of natural predators, we demonstrate the importance of incorporating sex-biased wildlife management into contemporary conservation plans. Where management attempts to replicate the effects of 'missing' predators, efforts should be made to monitor ungulate ASR and synergistically complement existing predator guilds.

KEYWORDS

carnivore, herbivore, predator, prey, prey selection, sex-bias, wildlife management

1 | INTRODUCTION

The adult sex ratio (ASR) of ungulate populations drives multiple aspects of their behaviour, ecology and life history, including individual sex roles and community breeding dynamics (Bowyer et al., 2020; Kappeler et al., 2023; Székely et al., 2014). For this reason, understanding ASR and its influence on population growth (e.g. mating choice, birth rates) is of central importance for biodiversity conservation (Mysterud et al., 2002). Many causes have been postulated to explain differences in ungulate ASR, including sex-specific biases in birth sex ratio, migration rate and vulnerability to mortality (Berger & Gompper, 1999; Schacht et al., 2022). However, the complexity and context-dependency of multiple drivers, often acting simultaneously, have made it challenging to discern and incorporate ungulate ASR into contemporary conservation strategies (Kappeler et al., 2023; Schacht et al., 2022).

Predation has long been highlighted as one key driver of ASR in large mammals. Darwin (1872) first postulated that predators may influence the ASR of their prey species either via direct (consumptive) or indirect (non-consumptive) effects (Figure 1). For example, in a global meta-analysis, large carnivore predation rates were biased towards males in 23 of 31 ungulate species (Berger & Gompper, 1999). Such sex bias has important implications for explaining differences in animal longevity. For instance, male kudu (*Tragelaphus strepsiceros*) in Kruger National Park, South Africa, are significantly more vulnerable to predation by lions (*Panthera leo*), with females living 1.6 times longer on average (Owen-Smith, 1993). This disproportionately high mortality of males contributes significantly to the typical female-dominated structure of many large ungulate species (Berger & Gompper, 1999), and an absence of predators may lead to an unnaturally high proportion of males in the population (Figure 1a; O'Kane & Macdonald, 2017).

Predators may also indirectly cause changes to prey ASR via sex-biased alterations to animal movement, nutrition, density, social dynamics or vulnerability to disease, which impact individual survivorship and fecundity (Figure 1b; Kappeler et al., 2023; Makin et al., 2017; Ruckstuhl & Neuhaus, 2002; Schacht et al., 2022). For example, by altering resource accessibility, predators can induce different mortality rates between sexes (Toigo & Gaillard, 2003). At high densities in a feral horse population, feeding competition exerted additional nutritional stress on reproductive females, leading to higher mortality and a male-biased ASR (Regan et al., 2020). Similarly, landscapes of fear generated by predators may alter prey movement behaviours and resource availability differently between sexes. By comparing reserves with and without predators, O'Kane and Macdonald (2017) demonstrated that kudu, impala (*Aepyceros melampus*) and blue wildebeest (*Connochaetes taurinus*) significantly increased sexual segregation in predator-laden environments but displayed more overlap in the absence of predators. Prey species are not, however, passive agents to the effects of predators, and it has been argued that mothers can also adjust their sex ratios at birth to best optimise gene flow (Trivers & Willard, 1973). For example, under conditions of abnormally high male density, female impala displayed a primary male: female sex ratio of 0.72 to increase female abundance (O'Kane & Macdonald, 2017). While the generality of this process remains equivocal (Schindler et al., 2015), there are evidently multiple, often entwined pathways through which natural predators may influence the ASR of prey species.

Today, humans are considered super-predators (Zanette et al., 2023), exerting pervasive direct and indirect influences on animal communities, including ungulate ASR. For example, sex-biased culling of individuals during trophy hunting or targeted harvesting can considerably alter ungulate ASR (Figure 1c; Ginsberg & Milner-Gulland, 1994; Milner et al., 2007). Humans also influence natural

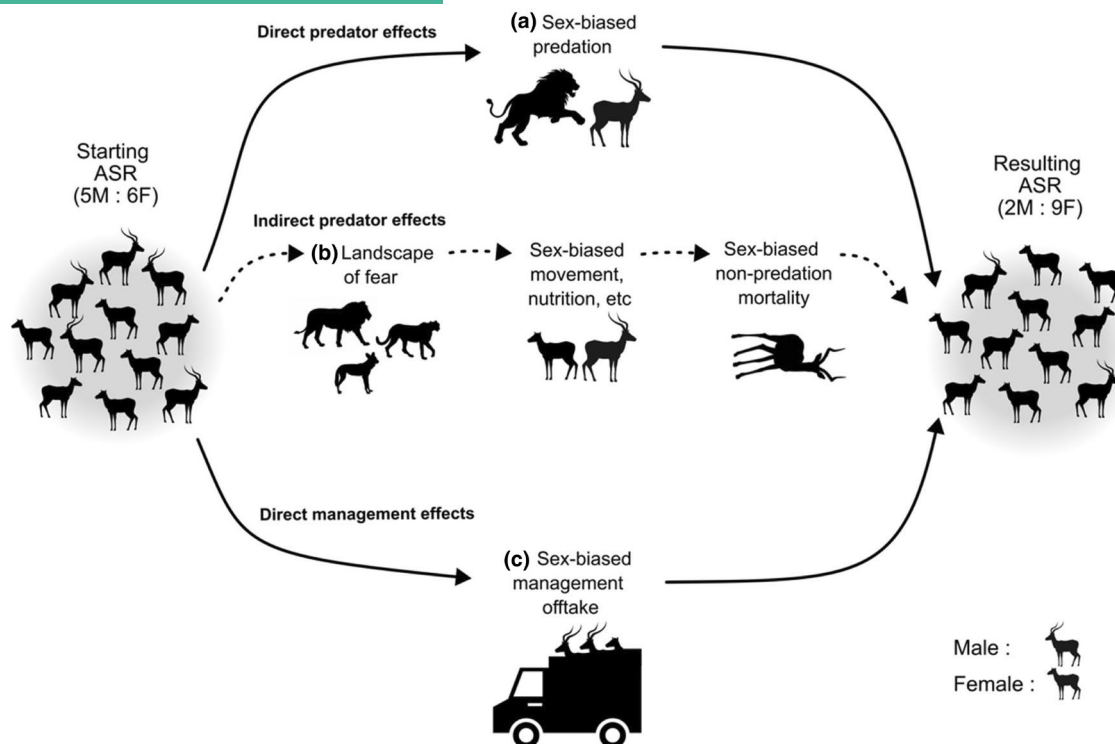


FIGURE 1 Both predators and wildlife managers can influence the adult sex ratio (ASR) of ungulate species through direct and indirect mechanisms, including sex-biased predation, landscapes of fear and offsite removal or culling. Wildlife managers may also indirectly influence ungulate ASR by modifying the natural predator guild and behaviours within a landscape.

predator effects; most notably, by causing local predator extinctions. Across the world, many ecosystems have been defaunated of some or all of their large carnivore species (Ripple et al., 2014). As different predators have different optimal prey body size ranges and diets (Hayward & Kerley, 2008), the characteristics and composition of the remaining predator guild will correspondingly influence outcomes for prey ASR.

While the most direct anthropogenic impacts on ungulate ASR have long been examined (e.g. the influence of trophy or selective hunting; Milner et al., 2007), much less attention has focused on how management strategies may replicate 'natural' predator impacts in the absence of large carnivore populations. In many ecosystems, wildlife managers already fulfil some of the roles of missing predators (e.g. by culling or removing animals to prevent overgrazing; Figure 1c; Abraham et al., 2021). But should wildlife removal or supplementation be biased towards one sex? And if so, by how much? For instance, anthropogenic hunting often deviates deer ASR from its 'natural' ratios, but feedbacks between sex-selective culling and population densities can rectify this (Clutton-Brock & Lonergan, 1994). Learning how to work synergistically with remaining predator guilds to replicate 'natural' drivers of ungulate ASR is a challenging but important step towards better ecosystem management (Kappeler et al., 2023).

Here, we capitalise on a fenced wildlife reserve in the Kalahari that is divided into two sections—but with similar environmental conditions and ungulate communities—to isolate the impacts of different predator guilds (lion vs. cheetah/wild dog) and management interventions

on ungulate ASR. We hypothesise that predators will influence the ASR of their preferred species directly via (i) sex-biased predation rates, or indirectly via (ii) sex-biased changes in prey behaviour, nutrition or body condition. We evaluate the effect of management intervention on large herbivore ASR through wildlife removal and to what degree this has replicated natural predator effects.

2 | METHODOLOGY

2.1 | Study site

Tswalu Kalahari Reserve is a 110,880 ha fenced wildlife reserve located at $-27.26, 22.45$ in the southern Kalahari, South Africa. Prior to 1995, Tswalu comprised ~40 domestic livestock farms, but was converted to a wildlife reserve by the removal of internal fences and associated infrastructure. Today, Tswalu comprises two main sections divided by an electrified fence; the Greater Korannaberg section (92,231 ha) and the Lekgaba section (18,649 ha) (Figure 2a). Similar ungulate communities occur in both sections at variable densities. The Korannaberg section, however, harbours cheetah (*Acinonyx jubatus*; ~ 4.3 ind/100 km⁻²), African wild dog (*Lycaon pictus*; ~ 0.4 ind/100 km⁻²) and in 2020–21, eight spotted hyaena (*Crocuta crocuta*) were introduced. We do not, however, include spotted hyaena in our analysis as they occur at low densities and have been resident for a shorter period of time. The Lekgaba section, in contrast, supports two prides of lion (*Panthera leo*; ~ 5.9 ind/100 km⁻²).

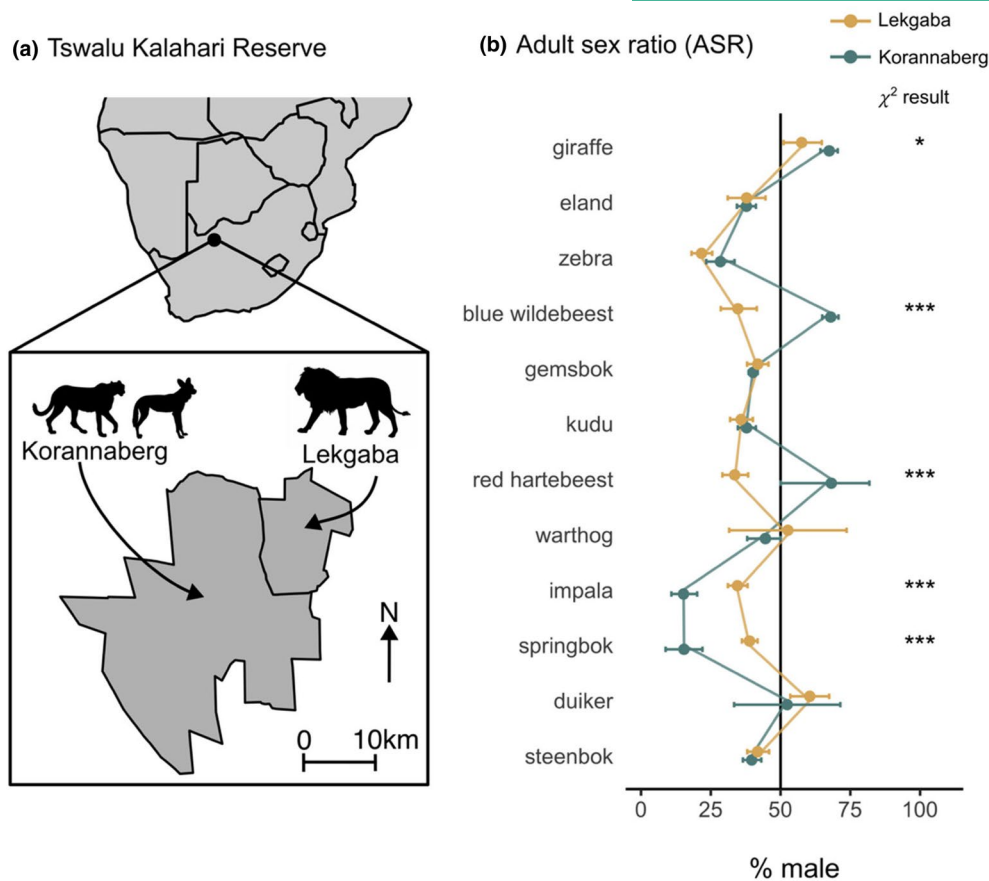


FIGURE 2 (a) Tswalu Kalahari Reserve, South Africa, highlighting the different predator guilds of the Korannaberg and Lekgaba sections. (b) Adult sex ratio (ASR)—represented as a percentage of males within each population—of large herbivore species resident within the Korannaberg and Lekgaba sections of Tswalu observed during the dry season. Error bars represent 95% confidence intervals generated from a 1000-fold bootstrapping procedure. Species with significantly different ASR based on chi-squared tests (χ^2) are highlighted, where $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).

Leopard (*Panthera pardus*), black-backed jackal (*Lupulella mesomelas*) and brown hyaena (*Parahyaena brunnea*) are resident at similar densities in both sections (Webster & Abraham, 2021).

Based on the status of both vegetation and ungulate communities, Tswalu management periodically removes or supplements ungulate individuals (Abraham et al., 2021). In the absence of lions, this management intervention has primarily focused on removing large-bodied species from the Korannaberg section. The specific number of animals removed was calculated based on the difference between stocked large animal units (LAUs) and the ecological carrying capacity, determined by mean annual rainfall and vegetation surveys (van Rooyen & van Rooyen, 2022). To ensure that other possible environmental drivers of ungulate ASR (e.g. resource availability; Toigo & Gaillard, 2003) were comparable between the Korannaberg and Lekgaba sections of Tswalu, we compared the availability of water, artificial mineral licks, forage nutritional quality and rainfall between sections (see Text S1; Table S1; Figure S1), finding no statistical difference between sections. As a result, Tswalu offers a unique opportunity to isolate the effects of predation and management on ungulate ASR.

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

2.2 | Ungulate abundance and adult sex structure (ASR)

Tswalu undertakes an aerial census of large herbivore species >10kg in March–April annually (see Text S2 and Abraham et al. (2023) for detailed methodology and Table S2 for associated herbivore densities). For many species, however, animal sex cannot be reliably quantified during aerial surveys (Ancona et al., 2017; Schuette et al., 2018). Consequently, we conducted five detailed ground-based large herbivore demographic surveys in July–August 2021, July 2022, July 2023, February 2024 and September 2024. Demographic assessments were conducted on eight pre-determined transects in the Korannaberg section (762.2km) and four transects

in Lekgaba (310.4 km). Effort was made to proportionally cover different habitat types across Tswalu (Figure S2; van Rooyen & van Rooyen, 2022), although fewer roads existed in mountain regions. Two experienced observers were equipped with binoculars and stood elevated in the back of an open Toyota Landcruiser moving at a speed of 15 km/h. Upon sighting, the age/sex/body condition of all individuals was reported. Animals were categorised as adults, sub-adults or juveniles depending on size, horn length, coat colour/pattern. Animals were sexed using dimorphic characteristics, including differences in size, presence or absence of horns, characteristics of horns and visibility of testes/penis sheath/mammary glands (Skinner & Chimimba, 2005). Specific animal groups may be attracted to trails and bias results (Ancona et al., 2017); however, the sparse vegetation at Tswalu generally allowed observation over large distances. We examined surveys individually and also combined data from all surveys 2021–2024 to calculate the % male for 12 large ungulate species in each section of Tswalu. To generate a central estimate and 95% confidence intervals, we bootstrapped this procedure 1000 times using sampling with replacement. As our data were categorical, we used a chi-squared test (χ^2) to examine the statistical difference ($p < 0.05$) in herbivore species ASR between sections.

2.3 | Predator consumptive effects: Prey preference and sex bias

To understand the consumptive effects of predators on large herbivore ASR, we utilised a comprehensive predator–prey kill database opportunistically collected by wildlife guides and managers at Tswalu during the period 2019–2024. Upon sighting, information pertaining to prey location, species and sex was recorded in Earth Ranger (<https://www.earthranger.com>). We calculated the Jacobs prey preference index (–1 avoided to 1 preferred; Jacobs, 1974) of large herbivore species (>10 kg) for lions, cheetahs and wild dogs at Tswalu. This approach compares the number of kills of a prey species with its proportional abundance in the landscape, as calculated by Equation (1):

$$D_{ij} = \frac{r_{ij} - p_{ij}}{r_{ij} + p_{ij} - (2 \times r_{ij} \times p_{ij})}, \quad (1)$$

where D_{ij} is the Jacobs' index of prey species i in section j , r_{ij} is the proportional kill rate of prey species i in section j from the guide kill database, and p_{ij} is the proportional abundance of prey species i in section j , averaged from the aerial census survey during the period 2019–2024. Plains zebra (*Equus quagga*) and mountain zebra (*Equus zebra*) were not consistently differentiated in the kill database and are thus combined here and throughout. We calculated a central estimate and 95% confidence intervals by bootstrapping this procedure 1000 times using sampling with replacement. We recognise that guide-reported databases may contain reporting biases (e.g. underreporting of smaller animals due to quick degradation of carcasses by scavengers such as brown hyaena (*Parahyaena brunnea*); Marker et al., 2003). We therefore also compared the results observed at Tswalu to continental averages (Hayward & Kerley, 2008).

Where clear identification could be made, guides also reported the sex of prey species. However, in some cases, animal sex could not be determined due to issues of visibility or carcass degradation. Ideally, we would have calculated predation sex bias for each species individually, but as some species had few (<10 observations), we grouped prey species into three groups based on the above predator–prey preference: lion-preferred kills (gemsbok-giraffe), all-preferred species (warthog-kudu) and cheetah-preferred species (steenbok-impala). We then calculated sex bias in predation rate for (i) each prey group and (ii) prey species with sufficient information ($n > 20$) individually, using Equation (2):

$$S_{ij} = \frac{m_{ij} - q_{ij}}{m_{ij} + q_{ij} - (2 \times m_{ij} \times q_{ij})}, \quad (2)$$

where S_{ij} is the sex preference of prey group/species i in section j (–1: female preferred to +1: male preferred), m_{ij} is the proportional kill rate of males for prey group/species i in section j from the guide kill database, and q_{ij} is the proportional abundance of males for prey group/species i in section j , averaged from the herbivore demographic surveys conducted between 2021 and 2024. We again generated a central estimate and 95% confidence intervals by using a 1000-fold bootstrap procedure using sampling with replacement.

To compare the outcome of our results at Tswalu to other locations, we undertook a semi-systematic literature search to examine sex biases of large African carnivores (>30 kg): cheetah, leopard, lion, spotted hyaena and wild dog. We first used the Web of Science (All Databases) with the search terms ['predator', 'prey', 'Africa', 'sex bias'] on 29 March 2024. This search yielded 2088 peer-reviewed papers, of which 20 were relevant based on the following criteria: studies must have compared predation rates to surveyed abundances and be located in Africa. In addition, we used Research Rabbit to extend our search to include papers not found using Web of Science but that were closely related. This search identified 8 additional papers (see Table S3).

2.4 | Predator non-consumptive effects: Prey herding behaviour, nutrition and body condition

Predators may exert non-consumptive effects on prey ASR via sex-specific changes to behaviour, nutrition or body condition, with subsequent impacts for survivorship and fecundity (O'Kane & Macdonald, 2017; Owen-Smith, 1993). To evaluate such effects on ungulate populations at Tswalu, we compared four non-consumptive metrics between sections: (i) herd size, (ii) sexual segregation, (iii) nutrition and (iv) body condition. Predator pressure has been shown to influence herding structures and segregation between sexes in ungulates (Makin et al., 2017; O'Kane & Macdonald, 2017; Ruckstuhl & Neuhaus, 2002). Such changes may subsequently influence sex-biased competition for resources and reproductive opportunities, which may alter animal nutrition and body condition. Ungulate herd size was calculated from aerial surveys 2019–2023; social segregation from ungulate demographic surveys 2021–2024 using equation S1

from (Conradt, 1998); nutrition based on faecal nitrogen, phosphorus and sodium in three species (springbok, kudu and blue wildebeest) (Abraham et al., 2023); and body condition across ungulate species (scored from 1 to 5 based on visual assessment). See Text S2 for details of specific methodologies. While our non-consumptive metrics do not provide a direct link to ungulate ASR, they encapsulate broad changes in animal behaviour and health, which have been linked to differences in ungulate ASR and primary sex ratios at birth (O'Kane & Macdonald, 2017). If large differences emerge between sections, it is likely that ungulate ASR is affected. To statistically compare metrics between sections, we used a Wilcoxon rank sum test.

2.5 | Management effects: Wildlife offtake and sex bias

Management protocol was to generally remove/supplement animals at the sex ratio proportional to their present occurrence (i.e. to not alter sex ratios; van Rooyen & van Rooyen, 2022). However, herbivore demographics were not studied at TKR prior to 2021, and it is therefore possible that management actions may have deviated from the actual sex ratios. Offtake has primarily been undertaken in the Korannaberg section (no lion), where ~1000 large herbivores were removed per year during the period 2010–2020 (Abraham et al., 2021). During the period 2022–2024, coincident with some of our herbivore demographic surveys, however, no animals were removed from this section. Nevertheless, as large herbivore individuals may be long-lived (>10 years; De Magalhães & Costa, 2009), the effects of management may still have a legacy on present-day herbivore ASR. Sex was identified and recorded for all adult individuals removed; we assume there was no active sex bias in offtake of juveniles. Notably, springbok and red hartebeest received considerable supplementation (>500 individuals) into the Korannaberg section in 2023 due to declining numbers. We therefore only consider demographic data and predator sex bias prior to supplementation for these species. Lekgaba was also occasionally supplemented with ungulates from the Korannaberg section. We compared the sex ratio of net animals removed/supplemented during the period 2010–2021 to the herbivore sex ratio observed during our herbivore demographic surveys. Where sex ratios deviate substantially, and a large proportion of the population is managed, it is possible that management has altered herbivore ASR.

2.6 | Comparison of predator and management effects on ungulate ASR

To examine possible differences in the direct impact of predators (Section 2.3) and management (Section 2.5) on ungulate ASR, we compared the number of male and female ungulate individuals killed by predators in each section to those removed by management during the period 2010–2021. Estimates for prey individuals killed by predators were calculated using Equation (3) (Hayward et al., 2007):

$$R_{ij} = \frac{D_{ij} \cdot p_i + p_i}{1 - D_{ij} + 2D_{ij}p_i} \times \sum K, \quad (3)$$

where R_{ij} is the predicted number of kills of ungulate population i when there is a total of $\sum K$ observed kills annually by predator j . D_{ij} represents the Jacobs' value of prey species i for predator j , and p_i is the proportional abundance of prey species i in that section. Predator abundance and kill rates at TKR were taken from Webster and Abraham (2021), and prey preference, sex bias and abundance from this study. Where possible, we used species-specific sex-bias results; in the absence of sufficient data, we used group averages (see Section 2.3). Total kills of males and females from each ungulate population were summed across predators (lion, cheetah and wild dog) and compared to management offtake.

3 | RESULTS

3.1 | Ungulate adult sex ratios

We observed 16,059 individual animals during ungulate demographic surveys conducted between 2021 and 2024, of which 96.5% and 82.2% had associated age and sex information, respectively. In general, most ungulate species were female-dominated, although notably giraffe were slightly male-dominated in both sections of the reserve (Figure 2b). Comparisons between sections revealed that ungulate species smaller than warthog generally had a smaller proportion of males in the Korannaberg section (cheetah/wild dog present), whereas species larger than warthog generally had a lower proportion of males in the Lekgaba section (lion present). Results of the chi-square (χ^2) test demonstrated that the male percentage of giraffe (*Giraffa camelopardalis*), blue wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus buselaphus*), impala (*Aepyceros melampus*) and springbok (*Antidorcas marsupialis*) was significantly different between sections at the $p < 0.05$ level (Figure 2b). These patterns were consistent between years and seasons surveyed (Figure S3).

3.2 | Predator–prey preference and sex bias

The predator–prey kill database included 308 kills by lion, 274 by cheetah and 221 by wild dog, of which 42.9% had associated prey sex information. Lion were found to have a similar preference for all ungulate prey species larger than impala and displayed a strong bias towards male individuals of these species (Figure 3). Cheetah preferred all ungulate species smaller than kudu, although with a notable avoidance of warthog, and displayed a mild preference for female individuals of their preferred species (Figure 3). Wild dog preferred ungulates within a narrow body size range between impala and red hartebeest and appeared to have no bias in sex preference of prey individuals (Figure 3). Analysis of predator sex bias at the species level revealed that individual prey species may deviate from

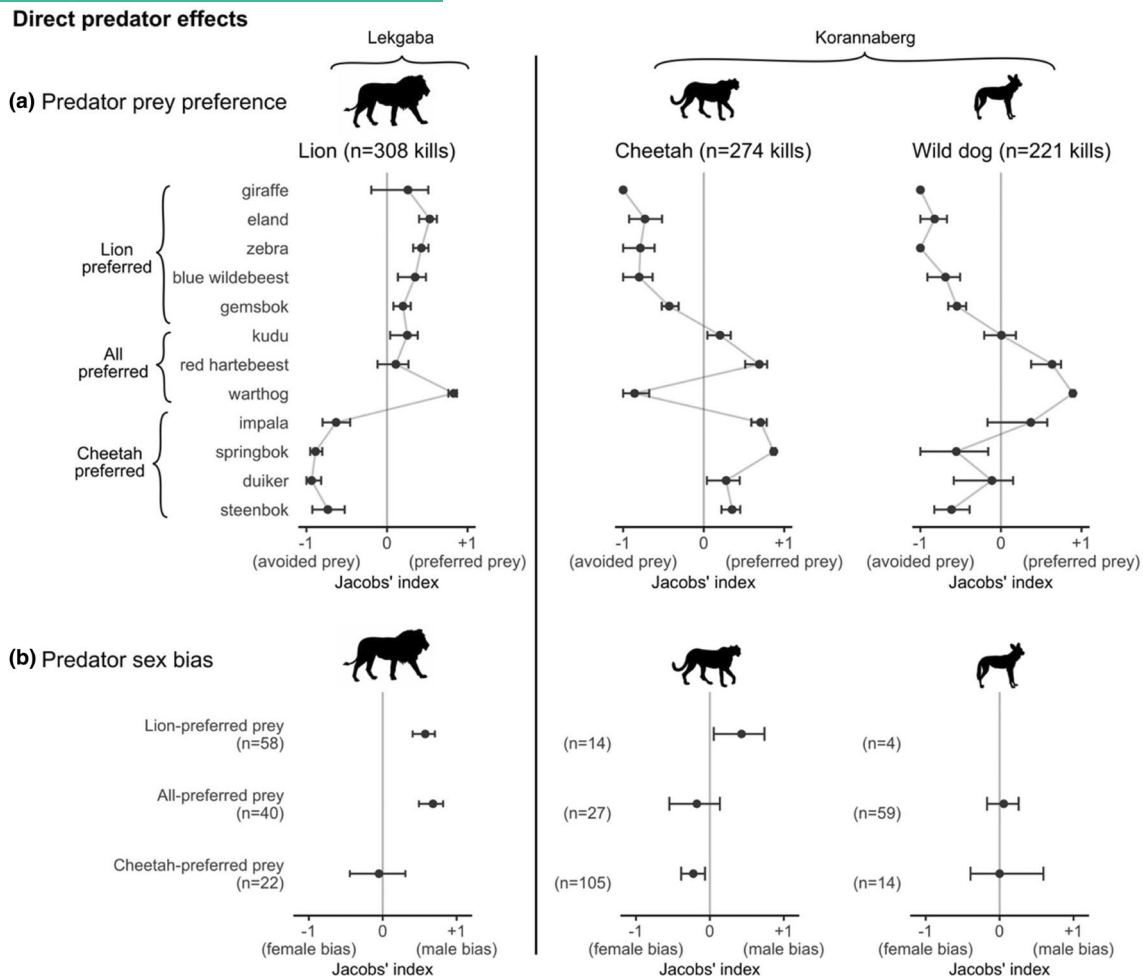


FIGURE 3 Predator consumptive effects on herbivore adult sex ratio at Tswalu. (a) Prey preference of large herbivore species (>10 kg) for lion (*Panthera leo*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*), calculated using Jacobs' preference index. Values closer to 1 indicate preferred prey, while values closer to -1 are avoided prey. Species are grouped into lion-preferred, all-preferred and cheetah-preferred groups. (b) Sex bias in prey kills for each prey group by lion, cheetah and wild dog, calculated using Jacobs' preference index. Values closer to +1 indicate male bias, while values closer to -1 show female bias. For inspection of predator sex bias of individual prey species and seasonal comparison, see [Figures S5](#) and [S6](#), respectively.

broad group trends (e.g. lion showed no sex bias for eland and zebra, while cheetah and wild dog had a mild preference for male gemsbok; [Figure S5](#)). We found no seasonal changes in prey preference or sex bias across predator species, except for cheetah, which displayed a greater sex bias towards females in the dry winter season ([Figure S6](#)).

3.3 | Predator effects on ungulate herding, segregation, nutrition and body condition

Ungulate herd size was larger when prey-specific predators were present in six of 12 species. For example, herd size significantly increased for zebra, blue wildebeest, gemsbok and red hartebeest in the section with lion, and increased slightly for impala and springbok in the section with cheetah ([Figure 4a](#)). Ungulate species that demonstrated herd size differences between sections also displayed accompanying differences in sexual segregation, with less sexual segregation generally occurring where predation pressure (and thus

herd size) was higher ([Figure 4b](#)). Analysis of faecal nutrients and herbivore body condition revealed no consistent difference between sections. Faecal N was statistically higher in Lekgaba for springbok, while P and Na were higher in Korannaberg for blue wildebeest and springbok respectively ([Figure S7a](#)). Similarly, male impala were found to have better body condition in Korannaberg, while male gemsbok and springbok and female giraffe, kudu and gemsbok were in better body condition in Lekgaba ([Figure S7b](#)). However, there was no consistent statistical effect of different predator regimes on nutrition or body condition metrics.

3.4 | Sex bias in management offtake and supplementation

During the period 2010–2021, 10,678 individuals across the 12 large ungulate species were removed from the Korannaberg section of Tswalu. In general, this corresponded to prey species preferred by

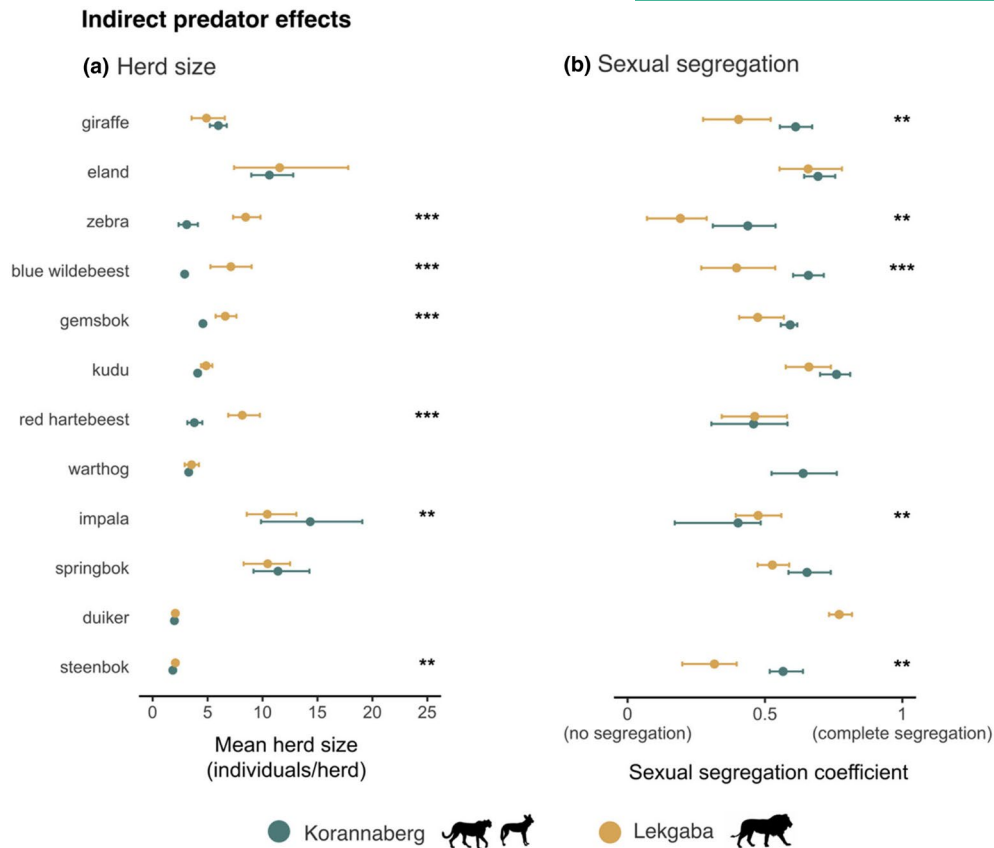


FIGURE 4 Predator non-consumptive effects on ungulate behaviour. Comparison between sections for (a) mean herd size calculated from aerial surveys 2019–2024. Species with significant differences are highlighted, where: $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***). (b) Sexual segregation calculated from (Conradt, 1998) using ground surveys 2021–2024. Error bars represent 95% confidence intervals generated from a 100-fold bootstrapping procedure. For inspection of differences in ungulate nutrition and body condition between sections, see Figure S7.

lions and in some years represented >20% of the resident population (Figure 5a). For these species (warthog and larger), the proportion of males removed was typically greater than that observed in the population during our herbivore demographic surveys (2021–2024) (Figure 5b). One notable exception was the blue wildebeest, which had a higher percentage of females removed during management offtake than that observed during our surveys. For springbok and impala, the sex ratio of animals removed was slightly biased towards females in comparison to our demographic survey. In Lekgaba, there was a net supplementation of 362 animals during the period 2010–2024 (369 supplemented; 67 removed). Management manipulation of herbivore populations, and thus subsequent impacts on herbivore ASR, was considerably smaller in Lekgaba than in the Korannaberg section (Figure S8).

3.5 | Natural predation and management offtake impacts on ungulate ASR

The combined effects of natural predation and management offtake were considerable for most ungulate populations, with >15% of the total population removed annually (Figure 6a). Warthog experienced

very high removal in Lekgaba; however, smaller species received very low removal in this section. Comparison between sections revealed that the proportion of male and female individuals removed from populations by predation and management offtake was not consistent within or across species. For example, in Lekgaba, natural predation of warthog, kudu and wildebeest by lions was strongly biased towards removing males, whereas management offtake of these species in Korannaberg removed a relatively greater proportion of females. Where management removed a large proportion of individuals, deviations from the 'natural' male: female kill ratios could be large (e.g. for gemsbok and blue wildebeest in Korannaberg; Figure 6b).

4 | DISCUSSION

4.1 | Predator and management effects on ungulate ASR at Tswalu

The combined impact of natural predation and management intervention has shaped ungulate ASR at Tswalu through multiple pathways. As a result, springbok, impala, red hartebeest and blue wildebeest

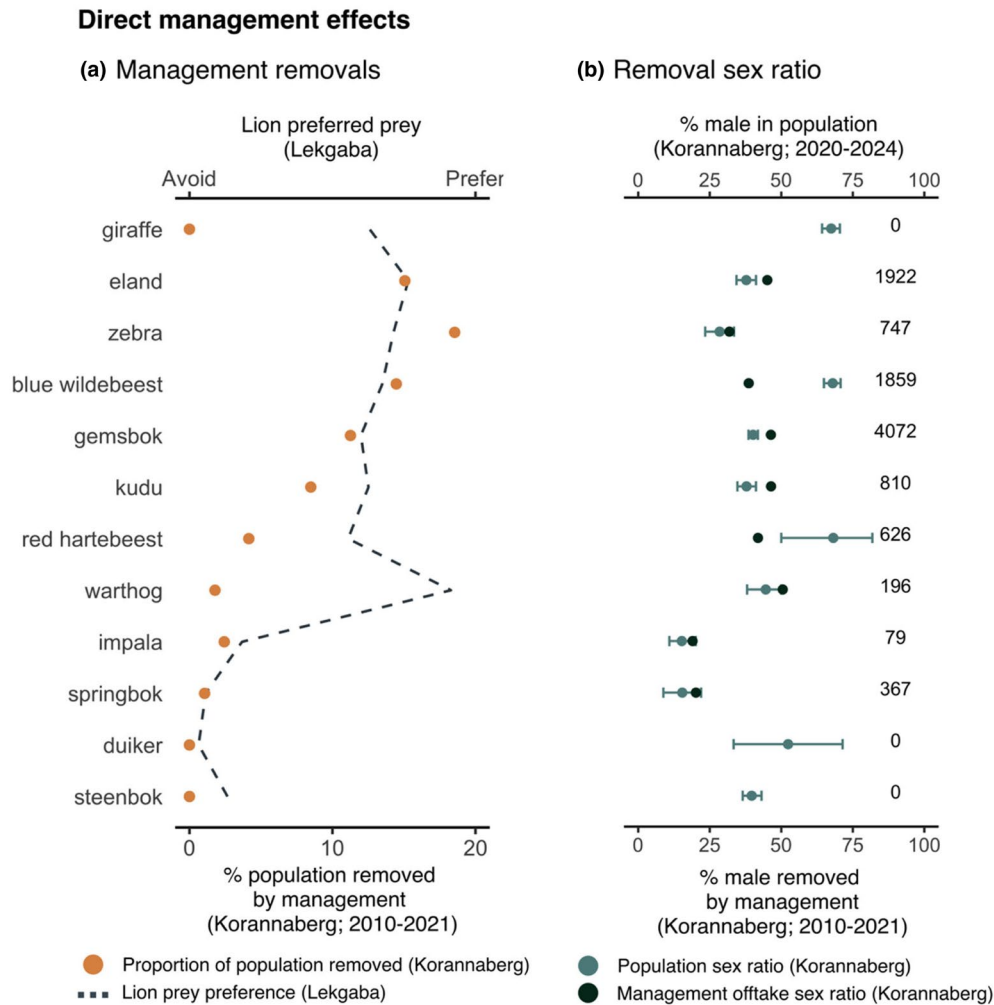


FIGURE 5 Wildlife management effects on ungulate adult sex ratio via offsite removal in the Korannaberg section of Tswalu Kalahari Reserve. (a) The mean proportion of ungulate population removed during the period 2010–2021 by management intervention (bottom x-axis) is similar to lion-preferred prey (top x-axis), with the exception of warthog (see [Figure 2a](#)). (b) The percentage of males that were removed by management (2010–2021) compared to the observed proportion of males in ungulate populations (2020–2024; [Figure 1b](#)). The total number of animals removed during 2010–2021 is highlighted. For inspection of management effects on ungulate populations in the Lekgaba section, see [Figure S8](#).

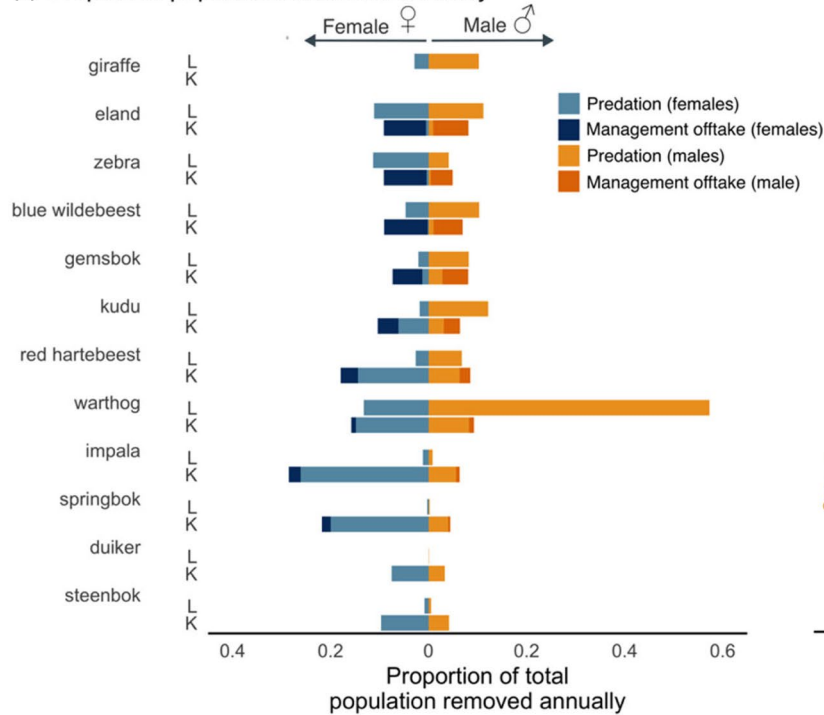
displayed statistically significant differences in ASR between sections ([Figure 2](#)). Together, predators and management removed 10%–30% of each ungulate population annually in both sections, except for species smaller than impala in Lekgaba, which received low levels of removal ([Figure 6a](#)). As lions displayed a particularly strong male bias for their preferred prey (i.e. species ranging in size from warthog to giraffe; [Figure 3](#)), more than twice as many male individuals were killed annually than females in Lekgaba ([Figure 6b](#)), despite representing only ~40% of the population ([Figure 2](#)). The exception to this was eland and zebra—species that tend to form larger herds when lions are present ([Figure S5](#); [Figure 4](#)). In the Korannaberg section, cheetahs and wild dogs demonstrated a strong preference for prey species <150kg, with cheetah showing a mild female sex bias in the dry season ([Figure 3](#); [Figures S5](#) and [S6](#)). An unexpected result was the high preference of red hartebeest by cheetahs; potentially the result of there being only a small resident population in this section. As ungulates in Korannaberg were also female-dominated,

more than twice as many female individuals were killed than males for smaller-bodied species in this section ([Figure 6b](#)).

In the absence of lions, wildlife management removed >1000 surplus large-bodied ungulates (>100kg) per year from the Korannaberg section between 2010 and 2021 to prevent overgrazing and ecosystem degradation (van Rooyen & van Rooyen, 2022). While the intention was not to alter ungulate sex ratios, wildlife management offtake appears to have somewhat fulfilled the sex-biased effects of natural predation by removing proportionally more males than observed in the population ([Figure 5b](#)). Animals removed from Korannaberg were generally sold to nearby communities, reserves and hunting farms. As male individuals generally command a higher price, there was some targeted removal of additional males for certain species (e.g. eland, kudu). In contrast, some species form large, female-dominated herds (e.g. blue wildebeest; [Figure 4a](#); Hunter & Skinner, 1998). As it requires more effort to round up many small bachelor herds than an equal number of individuals in a large

Combined direct impacts of predation and management

(a) Proportion population removed annually



(b) Sex ratio of removed animals

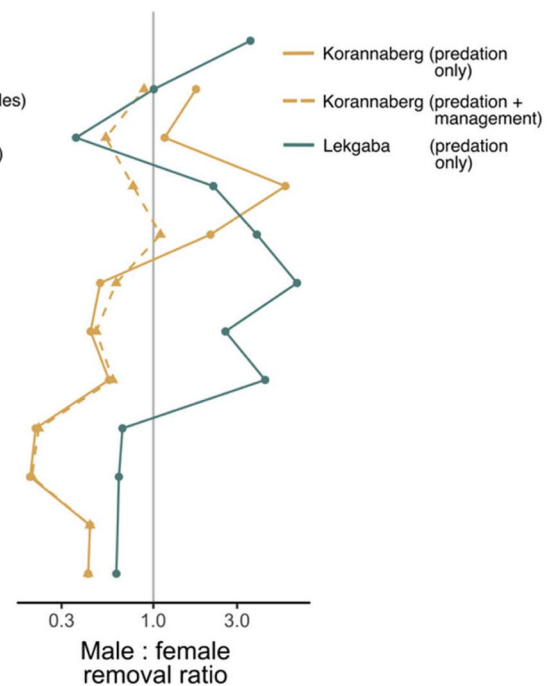


FIGURE 6 The combined impacts of natural predation and management offtake on ungulate adult sex ratio during the period 2010–2021. (a) Estimated mean removal of male and female ungulates from the Korannaberg (K) and Lekgaba (L) sections by natural predation and management offtake. (b) Estimated male: female removal ratio in Korannaberg by natural predators and in conjunction with management offtake, compared to natural predation in Lekgaba.

female-dominated group, this offers a plausible explanation for the female-biased offtake in this species.

We note, however, that management interventions have not simulated non-consumptive effects of predators (Figure 1). For example, we found marked differences in herd size and sexual segregation between sections for lion-preferred prey (Figure 4). This result aligns closely with previous reports showing that wildebeest aggregate into larger groups following predator reintroduction, but impala do not (Hunter & Skinner, 1998). In contrast, however, our results did not support the predator-risk hypothesis for increased sexual segregation under greater predation pressure (Ruckstuhl & Neuhaus, 2002). Evidence for such mechanisms is equivocal in African ungulates (Ruckstuhl & Neuhaus, 2002), and it is possible that the very high lion density (~5.9 ind/100km²) and high supplementary water and mineral resource availability at Tswalu (Abraham et al., 2023) may reduce intra-species competition for resources (Regan et al., 2020) and mitigate the benefits of segregation. The provision of supplementary resources at Tswalu may also explain why we did not find differences in nutritional status or body condition between ungulate populations (Figure S7). Without the provision of additional resources, changes in ungulate body condition may become more apparent, with knock-on effects on ungulate ASR. For example, during periods of drought, it has been recorded that male ungulates in the Kalahari experience higher levels of mortality (Knight, 1995).

The impact of altered ASR has important ramifications for ungulate social behaviours, health and population dynamics at Tswalu (Bowyer et al., 2020; Kappeler et al., 2023; Székely et al., 2014). In polygynous species, for example, population growth is fundamentally determined by the number of females at reproductive age (Åhman et al., 2014). Thus, for ungulates living in highly variable landscapes where population crashes are common, such as those caused by drought in the Kalahari (Knight, 1995), female-skewed populations can rebound more quickly than male-skewed populations. In light of this, the bias of cheetahs towards killing pregnant female individuals in the dry season (Figure S6) may have played an exacerbating role in the recent population declines of springbok and red hartebeest in the Korannaberg section of Tswalu (Webster & Abraham, 2021). It is, however, difficult to quantify the exact impacts of sex-biased removal by predators and management on behavioural changes and population growth. Ungulate populations have dynamic relationships with their environment, each other and the broader animal community. Furthermore, ungulates may potentially modify their primary sex ratio at birth to mitigate altered ASR back towards optimal ratios (O'Kane & Macdonald, 2017; Trivers & Willard, 1973). For example, using 30 years of data from harvested springbok in the Kalahari, Krüger et al. (2005) demonstrated that springbok mothers in superior body condition preferentially had more daughters, possibly to secure a more rapid fitness return. Given the complexity of

such inter-relationships, it is therefore critical that wildlife managers continue to routinely monitor ungulate ASR.

4.2 | Generalities and context dependencies of predator effects on ungulate ASR

In general, our results of predator sex bias at Tswalu align with observations from other sites across Africa (Figure S4; Table S3). For example, in our semi-systematic literature review, we found a sex bias towards males in 13/19 prey populations for lion, 4/6 populations for cheetah, but only 8/20 populations for wild dog (Table 1). Male ungulates are often considered more vulnerable to predation due to their riskier behaviours (e.g. solitary lifestyle or mating engagements), larger body size and compromised nutritional status during and after the rut (Berger & Gompper, 1999; Owen-Smith, 1993; Toïgo & Gaillard, 2003).

A notable difference, however, was that cheetah at Tswalu displayed a female bias for their preferred prey (steenbok-impala) during the dry season (Figure S6), in contrast to the general male bias observed elsewhere (Table 1; Table S3), including in the Kalahari (Mills, 1984). We do not have an immediate explanation for this unexpected finding. One possible rationale is that females are particularly vulnerable to predation during pregnancy due to reduced mobility and vigilance (Malcolm & Lawick, 1975). However, such effects would also be expected to occur in the nearby Kgalagadi National Park where males were preferentially killed at twice the rate of females (Mills, 1984). It should be noted, however, that cheetah density within the fenced Korannaberg section is approximately four times higher than free-ranging cheetah across the Kalahari (Mills, 1984); a result of cheetah relocations to Tswalu from nearby farms and low mortality rates due to the absence of lion (Webster & Abraham, 2021).

Clearly, predator biases and prey responses are dynamic, context-dependent and may change depending on environmental conditions, prey composition and density, predator group characteristics and individual-level idiosyncrasies, such as sociality and diet preferences (LaBarge et al., 2024). For example, at Tswalu, the difference in area

of Korannaberg and Lekgaba may be a confounding factor, despite the sections being environmentally comparable (Text S1; Table S1; Figure S1). As in many reserves, lion and wild dog populations are actively managed at Tswalu, with detailed information recorded on population size and predator ASR. This offers the opportunity to elicit the impact of predator group demographics (age, sex) on prey populations, including ASR. For example, it is known that lions alter prey choices (e.g. for buffalo) if males are present in the hunt (Hayward et al., 2007), while wild dogs at Tswalu appear to change their preferred prey size and sex depending on the number and age of pack members, switching from warthog to kudu/gemsbok when the pack size increases (pers obs). Our results, therefore, provide insights into the complexities of predator effects on ungulate ASR, but context-specific factors may influence their relevance to other areas (e.g. unfenced protected areas or reserves with different predator-prey assemblages).

4.3 | Challenges of replicating natural predator effects on ASR through management interventions

It is not difficult for wildlife managers to alter ungulate ASR. Indeed, today the ASR of almost all large ungulate populations is impacted—at least to some degree—by humans. For example, sex-selective culling regimes due to economic, ecological or hunter preferences can lead to unbalanced ungulate ASR (Milner et al., 2007). This is especially common in sexually dimorphic species, where habitat use, meat harvest and trophy value can differ considerably between sexes (Ginsberg & Milner-Gulland, 1994). The removal of predators from landscapes or provision of supplementary resources by humans has also indirectly led to altered ungulate ASR and unnaturally high levels of males in the population (O'Kane & Macdonald, 2017; Ripple et al., 2014). Yet, despite these numerous ways in which human activities can deviate ungulate ASR from its 'natural' position, it is not well understood how wildlife management practices can best facilitate 'natural' ASR in ungulates (Kappeler et al., 2023).

Despite the clear context-dependency of ungulate ASR dynamics, we have shown here that there are some generalities that can

Predator	Prey populations observed	Female bias	No clear bias	Male bias
Lion (<i>Panthera leo</i>)	19	2 (11%)	4 (21%)	13 (68%)
Leopard (<i>Panthera pardus</i>)	4	1 (25%)	0 (0%)	3 (75%)
Cheetah (<i>Acinonyx jubatus</i>)	6	0 (0%)	2 (33%)	4 (67%)
Wild dog (<i>Lycan pictus</i>)	20	7 (35%)	5 (25%)	8 (40%)
Spotted hyaena (<i>Crocuta crocuta</i>)	4	2 (50%)	1 (25%)	1 (25%)

TABLE 1 Sex bias in predation rates of large African predators on prey populations across sites in sub-Saharan Africa obtained from a semi-systematic literature review.

Note: For inspection of sex bias of individual predators on specific prey populations, see Table S3.

be used to inform wildlife management. For example, it is clear that lions (both at Tswalu and across Africa; [Figure 3b](#); [Table 1](#)) display a strong sex bias towards male prey individuals. Such evidence will be useful for conservation plans aiming to replicate the direct effects of apex predators on larger-bodied ungulate species. In contrast, evidence for sex bias by cheetah is equivocal and is instead useful for highlighting context dependencies and ecosystem connections. It is common practice for managers to monitor ungulate demographics (e.g. age; sex) in wildlife areas throughout the world. Here, we used labour-intensive ground surveys; for some groups (e.g. larger-bodied species), however, it may be possible to undertake broad-scale ASR assessments from the air (Ancona et al., 2017). Aggregating all such datasets will help elicit further generalities and reveal details that will be useful for fine-tuning adaptive management approaches. For example, does predator sex-bias change seasonally in relation to the availability, space-use and health/reproductive status of prey animals? Such knowledge will help wildlife managers from across a variety of ecosystems work synergistically with remaining predator guilds to replicate the direct effects of 'missing' predators on ungulate ASR. Ultimately, this will have important knock-on effects for fundamental biological processes (e.g. individual animal sex roles, community breeding dynamics) and biodiversity conservation (Kappeler et al., 2023; Schacht et al., 2022). While challenging, such efforts are an important step towards better ecosystem management.

AUTHOR CONTRIBUTIONS

Andrew Abraham and Andrea Webster conceived the ideas and designed the methodology; Andrew Abraham, Andrea Webster, Wendy Panaino, Dylan Smith and Olivia Jones collected the data; Andrew Abraham, Celesté Maré, Marcus Clauss and Elizabeth le Roux analysed the data; Andrew Abraham led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: <https://doi.org/10.6084/m9.figshare.30008959.v1> (Abraham et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Statistical comparison of environmental conditions between the Korannaberg and Lekgaba sections of Tswalu Kalahari Reserve. Only Mn concentration in trees was found statistically significant ($p < 0.05$), although this was not considered significant when a Bonferroni correction was applied.

Table S2. Mean and range [min, max] of abundance and density estimates of large ungulate (>10 kg) species for the period 2020–2023 in the Greater Korannaberg and Lekgaba sections of Tswalu Kalahari Reserve, South Africa. Values in brackets represent minimum and maximum estimates. Information pertaining to sensitive species (rhinos) has been omitted for security reasons. Some species (e.g. buffalo, roan and sable) only occur at low densities in the Greater Korannaberg section and have thus not been included in analysis of adult sex ratios.

Table S3. Sex bias in predation rate for large African carnivores assembled from our semi-systematic literature review. Sex bias was determined from individual literature sources, where ‘M’ indicates male bias, ‘F’ for female bias and ‘NONE’ for no bias or a preference not statistically significant. * are used to determine results that are statistically significant. Values without a * report a trend in sex bias from qualitative assessments (e.g. reported in paper discussions).

Figure S1. Environmental comparison between the Korannaberg and Lekgaba sections of Tswalu Kalahari Reserve. (A) Per unit area there are more permanent waterhole sites (and thus artificial mineral

lick locations) in Lekgaba. However, per ungulate individual, water/mineral lick availability is remarkably similar. (B) Wilcoxon-tests reveal no statistically significant ($p < 0.05$) differences in forage nutrient quality across 10 elements associated with ungulate health, except for Mn in C_3 plants (trees). (C) Wilcoxon-tests also reveal no statistical difference in mean annual rainfall between sections.

Figure S2. Routes driven during ungulate demographic assessments at Tswalu Kalahari Reserve. Black lines display the road network across Tswalu. Routes taken (8 in the Greater Korannaberg section and 4 in the Lekgaba section) are highlighted in red. Effort was made to proportionally cover different habitat types across the reserve. No roads travel over the Korannaberg mountains (habitat: Mtn shrubveld) and thus routes were chosen to travel along the bottom of mountain edges.

Figure S3. (a) Inter-annual comparison of adult sex ratio (ASR)—represented as percentage of males within each population—of large herbivore species resident within the Korannaberg and Lekgaba sections of Tswalu between 2021 and 2024. Error bars represent 95% confidence intervals generated from 100-fold bootstrapping procedure. Only results where >20 individuals were observed in both sections are reported. For each species, the number of years ASR was significantly different ($p < 0.05$) based on chi-squared (χ^2) tests are highlighted. Springbok, impala and blue wildebeest are consistently different across years. Giraffe were not found statistically different in any individual year, although males account for a greater proportion in each field survey and are thus statistically significant when years are combined (see Figure 1). Seasonal comparison of ASR in (b) Korannaberg and (c) Lekgaba for the year 2024, where two field surveys were undertaken at the end of the wet season (February) and end of the dry season (September). In general, results are similar between seasons, although notable discrepancies occur for springbok, impala and eland. We note, however, that these species tend to form large herds segregated by sex. It is therefore possible that observed differences were driven by low sample size rather than actual changes in ungulate ASR throughout the season.

Figure S4. Comparison of predator–prey preference at Tswalu Kalahari Reserve and continental averages for lion (*Panthera leo*), cheetah (*Acinonyx jubatus*) and wild dog (*Lycan pictus*). Continental averages taken from Hayward et al. (2005), Hayward et al. (2006a) and Hayward et al. (2006b).

Figure S5: Sex bias in prey kills for lion, cheetah and wild dog, calculated using Jacob's preference index. Values closer to +1 indicate male bias, while values closer to -1 show female bias. Prey species shown have >20 observations with associated sex information from guide reported predator–prey kill database.

Figure S6. Seasonal predator consumptive effects on herbivore adult sex ratio at Tswalu. (a) Prey preference of large herbivore species (>10 kg) for lion (*Panthera leo*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycan pictus*), calculated using Jacob's preference index by season. Values closer to 1 indicate preferred prey, while values closer to -1 are avoided prey. Summer (wet season) and winter (dry season) seasons are defined by November–April and May–October, respectively. Species are grouped into lion-preferred, all-preferred and cheetah-preferred groups. (b) Seasonal sex bias in prey kills for each prey group by lion, cheetah and wild dog, calculated using Jacob's preference index. Values closer to +1 indicate male bias, while values closer to -1 show female bias. Only groups with $n > 10$ are shown. Overall, there is remarkably little seasonal variation in either prey preference or sex bias across large carnivore species, except for cheetah preferring female prey during the dry season, but displaying no sex preference during the wet season.

Figure S7. Predator non-consumptive effects on herbivore adult sex ratio at Tswalu Kalahari Reserve (TKR). (A) Comparison of herbivore nutrition, based on concentration of faecal nitrogen (N), phosphorus (P) and sodium (Na), between sections of TKR for a lion-preferred prey (blue wildebeest; *Connochaetes taurinus*), all-preferred prey species (kudu; *Tragelaphus strepsiceros*) and cheetah-preferred species (springbok; *Antidorcas marsupialis*). (B) Comparison of herbivore body condition between sections of TKR for male and female individuals of large herbivore species. Note: body condition scores have been jittered from 0.5 scoring increments for visual effect. Significant differences between sections for both faecal and body condition scores are denoted, where not significant (ns), $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***). Across both faecal and body condition metrics, predators appear to have little effect on herbivore nutrition and body condition.

Figure S8. Sex ratio of large herbivores supplemented into the Lekgaba section of Tswalu Kalahari Reserve during the period 2010–2024, compared to the adult sex ratio of large herbivores surveyed in Lekgaba during the period 2021–2024. Numbers to the right highlight the total number of animals supplemented in Lekgaba during 2010–2024.

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