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Response of southern African ungulate species to supplementary feeding during drought: species-specific differences in relative use, food choice, and intraspecific behavioural interactions

Running heading: Responses of ungulates to supplementary feeding

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In southern Africa, climate change is increasing drought severity and duration. One way to mitigate drought-induced food shortages is supplementary feeding, but ungulate responses are largely unstudied. Here, we analyse ~250 hours of video footage from camera traps at feeding stations in South Africa during a year when rainfall was ~50% of the decadal average. Feeding station usage was highly uneven: eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), sable (*Hippotragus niger*) and white rhino (*Ceratotherium simum*) were over-represented relative to their local population; impala (*Aepyceros melampus*), blesbok (*Damaliscus dorxas phillipsi*) and zebra (*Equus quagga*) were under-represented. In total, 81% of individuals at feeding stations fed (0-90% for different species). Guarding behaviour was observed, especially by eland and kudu, potentially excluding other (smaller) species. Overall, 17% visits involving ≥2 individuals involved intraspecific aggression (highest for sable (40%) and eland (27%); low/absent otherwise); there were very few (n=6) interspecific encounters. Lucerne and teff hay were consumed more frequently than Boskos (pellets), which was favoured by non-target primates and ungulates showing guarding behaviour. As benefits of feeding are unequal, and can encourage guarding and intraspecific aggression, we suggest feeding should be done with caution, especially if the aim is to benefit specific species.

Keywords: body condition, feeding stations, supplemental food, starvation

Introduction

Climate change is a substantial threat to biodiversity in areas already classified as arid or semi-arid (Knapp et al., 2008; Duncan *et al.,* 2012). In southern Africa, drought is a natural part of bushveld and savannah ecosystems, where seasonality is often driven more by changes in rainfall than by changes in temperature (Staver et al., 2011). However, more intense periods of drought, especially if these are widespread spatially or prolonged, can have profound ecological consequences. A reduction in availability and nutritional quality of vegetation can directly impact herbivores by causing loss of body condition, increased morbidity, or mortality (Marshal *et al.,* 2012), which can lead to population decline, genetic bottlenecks and, ultimately extirpation (Williamson and Mbano, 1988; Young 1994; Knight 1995; Duncan *et al.,* 2012; Abraham *et al.,* 2019).

Previous studies of population crashes linked to drought in southern Africa include the loss of 50,000-80,000 blue wildebeest (*Connochaetes taurinus*) in Central Kalahari Reserve, Botswana in 1983 (Williamson and Mbano, 1988), and the ten-fold decline of roan (*Hippotragus equinus*) in Kruger National Park, South Africa (from 450 in 1986 to 45 in 1993: Harrington et al. (1999)). The Botswana wildebeest decline was causally linked to food depletion over multiple droughts, compounded by increased energy expenditure as animals moved long distances to find food and water. The Kruger roan decline was attributed to the combined impacts of drought-induced food shortages, and associated increases in competition, predation, and disease. The ecological consequences of drought thus depend not only upon the severity, magnitude and duration of the drought itself, but also co-occurring stressors (Knight, 1995). Ecological consequences can also differ between trophic levels, with impacts often being more profound for herbivores than for carnivores or scavengers, which in the short-term might even benefit from weakened prey and increased carrion (Young 1994; Loveridge et al., 2006). Among herbivores, dietary niche is important; grazers and mixed-feeders are typically affected more than browsers (McNaughton and Georgiadis 1986; Walker et al., 1987; Duncan *et al.,* 2012). Impacts are also more likely to be magnified when animals cannot move across the landscape, because of fencing or other barriers (Knight 1995; Boone et al., 2006; Staver et al; 2019).

One way to mitigate drought-induced food shortages is supplementary feeding, especially in fenced reserves where the alternatives might be mass die-off (Young, 1994) or management culling (Walker et al., 1987). Although supplemental feeding of wildlife in southern Africa is not routinely practiced, anecdotal evidence, news reports, and practitioner periodicals suggest that it has been undertaken in several protected areas in times of drought, including for hippo in Gonarezhou National Park, Zimbabwe and for mixed grazers in the

Northern Cape of South Africa in a drought in 2019/20 (Ngcuka and Heiberg, 2020). Intuitively, supplementary feeding should improve individual body condition and survival, and indeed some studies have shown this to be the case, but it is far from inevitable (review by Milner et al., 2014 and references therein). There is also potential for unintended consequences, including altered behaviour, higher localised density of conspecifics, increased interspecific encounters, and spread of parasites and disease (Thompson et al., 2008; Sorensen et al., 2014; Murray *et al.,* 2016). Although there has been some very useful research on supplementary feeding for individual species in southern Africa (e.g. white rhino *Ceratotherium simum*: Cinková et al., 2017), almost all current knowledge on the effects of supplementary feeding on wild ungulates derives from studies of northern hemisphere species. Indeed all 101 papers included in the comprehensive review by Milner et al. (2014) came from North America (48) or Europe (53), while of the 115 papers considered by Murray et al. (2016) 102 were from North America and Europe, with 11 from Asia and just two from Africa (Central African Republic and Mauritius). Moreover, if supplemental feeding is being undertaken for multiple co-occurring ungulate species, it is vital that efficacy is considered at community level.

Given the paucity of studies on supplementary feeding of southern African ungulates, research on supplemental feeding in African contexts is urgently needed to understand benefits and costs of such interventions. This need is amplified both by the ecological and economic importance of such species and increasing risk of drought-induced wildlife declines in southern Africa because of climate change. Here, we provide initial baseline data on 20 ungulate species at supplemental feeding stations installed to provide short-term food at the end of an extended drought. We consider time spent at feeding station, food choice, body condition, and behaviour, including guarding and intraspecific aggression.

Methods

The study area is a 47 km^2 wildlife reserve in Northwest Province, South Africa, fully enclosed by a game-proof fence. The vegetation is a matrix of grasses and *Vachellia* scrub. The dominant tree and shrub species are umbrella acacia (*Vachellia tortilis*) and sicklebush (*Dichrostachys cinerea*), with some marula (*Sclerocarya birrea*). In an extensive grassland survey in 2019 (Goodenough et al., 2020) 45 grass species were identified on site. These were dominated by broad curly leaf (*Eragrostis rigidior*), common russet (*Loudetia simplex*), finger grass (*Digitaria eriantha*), wool grass (*Anthephora pubescens*), herringbone (*Pogonarthria squarrosa*), tassle three-awn (*Aristia congesta*) and wire grass (*Elionurus muticus*). The site is managed using a 4-5 year rotational block-burn, which encourages regeneration of vegetation and prevents late-successional (nutrient-poor)

Table 1 Species-specific visitation rates to feeding stations, and visit demography (number of individuals per visit, feeding rates, and food preferences). Reserve populations are given for all species except white rhino, where data have been withheld due to the species' vulnerability.

Reserve population (individuals 2019)	Common name	Scientific name	Number of visits	Time at feeding station (hr : min)	Time spent feeding (hr : min)	Number of individuals per visit			% of individuals that fed	% of feeding individuals using:		
						Mean	Min	Max		Taff/Lucerne	Boskos	Both
316	Blesbok	*Damaliscus dorxas phillipsi*	3	00:43	00:41	5.3	1	13	81	100	0	0
338	Blue wildebeest	*Connochaetes taurinus*	74	27:27	24:36	4.4	1	20	83	100	0	0
69	Eland	*Taurotragus oryx*	131	99:39	87:42	2.7	1	10	96	48	12	40
43	Gemsbok	*Oryx gazelle*	8	05:09	04:39	2.8	1	9	60	100	0	0
44	Giraffe	*Giraffa Camelopardalis*	10	00:45	00:03	1.8	1	4	17	100	0	0
154	Greater kudu	*Tragelaphus strepsiceros*	110	58:07	46:33	3.1	1	10	91	50	13	37
462	Impala	*Aepyceros melampus*	4	00:10	00:02	3.0	1	9	0	-	-	-
11	Nyala	*Tragelaphus angasii*	2	00:41	00:23	1.0	1	1	100	100	0	0
55	Red hartebeest	*Alcelaphus buselaphus caama*	2	00:02	00:00	1.0	1	1	0	-	-	-
13	Sable	*Hippotragus niger*	60	21:01	13:51	2.9	1	7	66	65	22	13
48	Tsessebe	*Damaliscus lunatus*	6	00:40	00:31	2.0	1	3	50	100	0	0
101	Warthog	*Phacochoerus africanus*	16	03:52	01:11	1.6	1	3	75	95	5	0
-----	White rhino	*Ceratotherium simum*	66	30:55	19:37	1.4	1	4	76	70	12	18
277	Zebra	*Equus quagga*	4	00:38	00:32	4.0	2	7	19	100	0	0

grasses dominating (Goodenough et al., 2017). The reserve supports 20 ungulate species with accurate population data sizes derived from comprehensive annual aerial counts, regular ground-based censuses, and offtake data (Goodenough et al., 2018). Overall stocking intensity in 2019 was 2,149 individual ungulates across the whole reserve (45.7 animals per km^2). The population sizes for all 14 species that ultimately used feeding stations, except for white rhino as a sensitive species, are given in Table 1. As regards predators, there are low numbers of caracal (*Caracal caracal*) and serval (*Leptailurus serval*) on the reserve but no resident big cats.

Daily rainfall has been recorded at the reserve since 1 Jan 2010. Over that period, 5-6 rainfall gauges distributed throughout the reserve have monitored rainfall, with these values averaged to give a daily value for the reserve. On 21 October 2019, the study area had received no rain for 180 consecutive days. This was the longest period without rainfall since records began almost a decade before. Moreover, the running record for rainfall for that calendar year was ~50% below the decadal average, albeit slightly higher than the worst drought year experienced on the reserve in 2015 (Fig. 1). The total precipitation in 2018 had also been below-average (Fig. 1) and, on a wider spatial scale, 2018-2019 was designated as a period of drought across South Africa by Wildlife Ranching South Africa (Kitshoff-Botha, 2019). The lack of rainfall had resulted in sparse nutrient-poor grassland and dry water courses, although water remained available in nine artificial pans supplied with pumped ground water. On 29 October 2019, for the first time in the reserve's 25-year history, 13 feeding stations were established and stocked with three foods: lucerne (alfalfa; *Medicago sativa*), teff hay (*Erogrostis tef*), and Boskos (a commercial pellet food comprising grasses, linseed (*Linum usitatissimum*), Acacia and sicklebush (*Dichrostachys cinerea*)). Lucerne and teff were provided in bales broken up around the feeding stations while Boskos was provided in old vehicle tyres to prevent pellets being scattered; food was replenished when 80-90% had been consumed. Locations were based on ease of access and close proximity to water in artificial pans. The feeding stations were used for one month, after which rains arrived. Camera traps were established at six feeding stations (Bushnell™ Trophy Aggressor cameras with a passive infrared sensor) to monitor usage. The cameras were set to record 10 second video clips, triggered by movement, using visible light diurnally and infrared nocturnally with a 3-second gap between each video, which was necessary for data to be written to the SD card. Camera traps were used to monitor each of the six feeding stations for the first two weeks of the supplemental feeding period (a total deployment time of ~1000 hours). SD cards were changed and batteries were replaced periodically, usually when the feeding station was being checked and food replenished.

Overall 249hr 48mins of video footage was recorded as series of 10-second video clips. Consecutive footage was

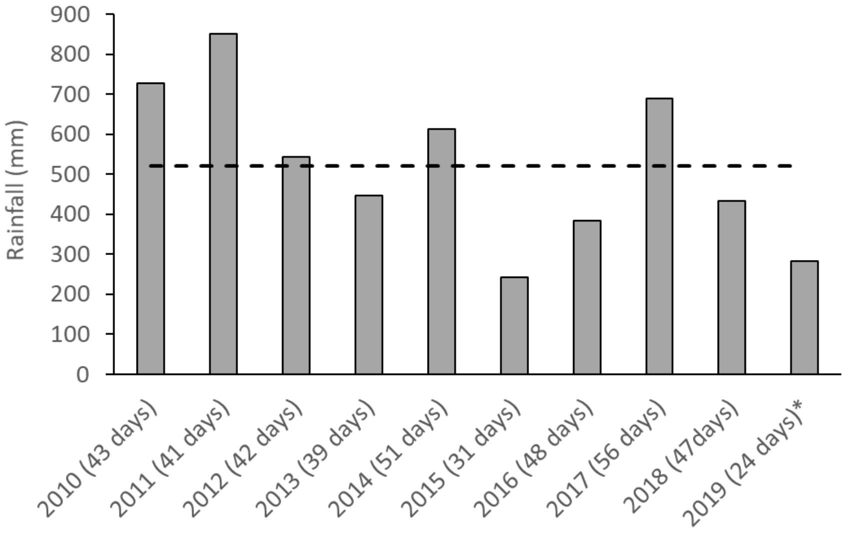

*Figure 1 Annual rainfall recorded at the study site, 2010–2019 inclusive, relative to the annual average of 521 mm across the decade (dashed vertical line). The number of days per year on which rain fell is given in parentheses. *Total until 21 October when the decision was taken to start supplemental feeding*

considered part of the same visit event if the same species was shown in multiple 10-second video clips that were sequential. The number of individuals present, group composition, and individual markings were used as additional verification that multiple videos were part of the same visit event. When >15 min elapsed between sequential videos, this was classified as a separate visit event even if the same species (or individuals) were shown. Although this time gap was arbitrary, we needed to distinguish different visits given that footage was not continuous but split across multiple movement-triggered videos.

For each visit, we recorded: (1) species; (2) number of individuals; (3) total time at the feeding station; (4) whether feeding occurred; (5) how many individuals fed; (6) total time at least one individual fed. Where possible, we recorded individual-level data, including: (1) body condition; (2) food consumed (teff/lucerne, which could not be differentiated on videos, or Boskos); (3) any intraspecific aggressive behaviours classified as per Powell *et al.* (2013). Condition was evaluated using resources collated and disseminated by the Association of Zoos and Aquariums Nutrition Advisory Group (2020); a 1-5 ordinal scale whereby 1=emaciated, 2=poor, 3=normal, 4=fat, 5=obese. Example images of relevant species were consulted when assessing condition and and all assessments were undertaken by one person (co-author EGS) to eliminate inter-observer variation.

To compare observed distribution of feeding station use by each species relative to the frequency of each species within the overall ungulate community (i.e. the expected distribution), chi square goodness of fit tests were used. Two iterations were undertaken, firstly using the number of recorded visits of each species to the feeding stations and secondly using the amount of time each species spent at the feeding stations. To analyse whether there was a statistically significant association between individual body condition and whether that individual fed or not, chi square test for association was used.

Results

In total, 519 feeding station visits were documented. This included 26 visits by vervet monkeys (*Chlorocebus pygerythrus*) (1-8 individuals per visit; mean =4) and 3 visits by chacma baboon (*Papio ursinus*) (2-9 per visit; mean = 5). These were documented but excluded from further analysis, which focussed solely on ungulates. Primates exclusively consumed Boskos. Of the 490 feeding station visits by ungulates, 484 involved a single species while 6 involved multiple species. Ungulates spent 249hr 48mins at the six monitored feeding stations relative to a total camera trap deployment period of ~1000 hours (i.e. ~25% usage). Overall, 200hr 22min of usage involved at least one individual actively feeding (Table 1). Usage of feeding stations was highly uneven, both in relation to uniformity and in relation to the relative species abundance within the ungulate community of the reserve, regardless of whether number of visits or overall time at feeding stations was used (Fig 2).

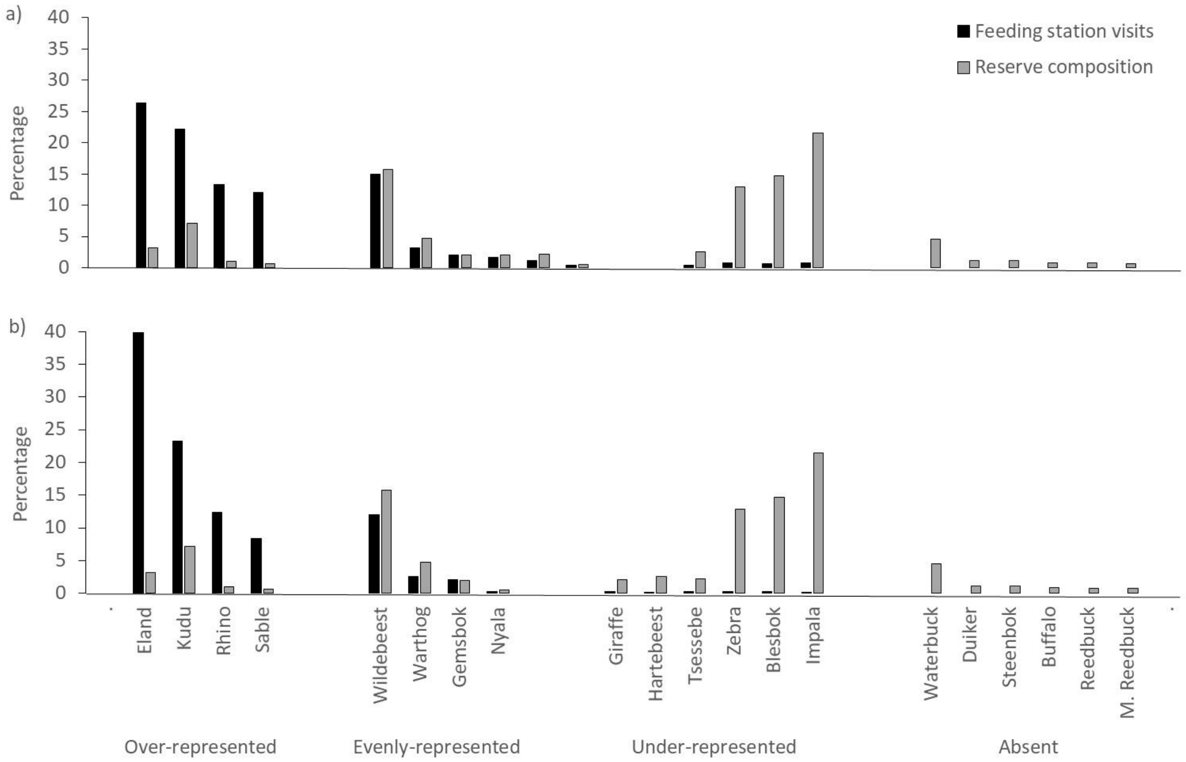

Figure 2 Feeding station usage measured in terms of (a) number of visits and (b) amount of time in relation to reserve ungulate species community. Six reserve species were never seen at feeding stations. M. Reedbuck =

mountain reedbuck (Redunca fulvorufula)

The non-uniform patterns of feeding station usage compared to relative abundance in ungulate community composition were statistically significant (chi-square goodness of fit: visits $\chi^2 = 2,715$; d.f = 19; $P < 0.001$; time = $\chi^2 = 111,286$; d.f = 19; $P < 0.001$). This pattern was driven by eland, kudu, sable and white rhino being over-represented, while impala, blesbok and zebra were notably under-represented. Six species were absent, of which three were associated with marginal vegetation around natural water sources (waterbuck (*Kobus ellipsiprymnus*), reedbuck (*Redunca arundinum*), and mountain reedbuck (*Redunca fulvorufula*)). The amount of time individuals were present at a feeding station but not actively feeding varied greatly between species (Fig. 3), as did group size (Table 1).

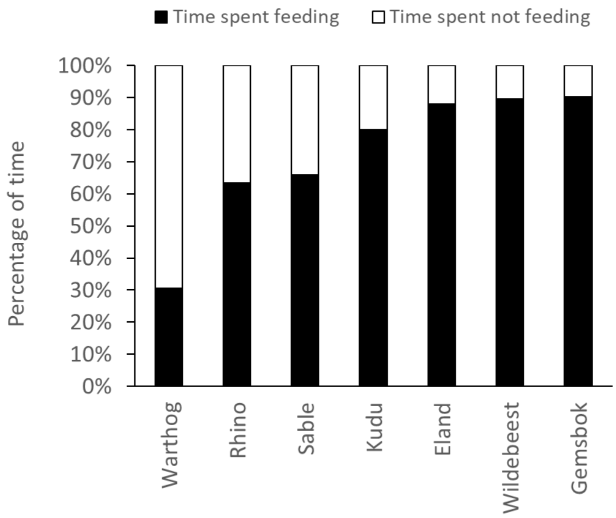

Figure 3 Relative percentage of time at feeding station devoted to feeding (at least one individual feeding) versus not feeding. Only species where there was >3 hr of footage were included to avoid percentage estimates potentially being biased by low sample sizes.

We were able to collect individual-level feeding data on 1,431 animals from camera trap footage. Overall, 81% of animals fed but this varied from 0% for impala and red hartebeest (i.e. despite being present, no individuals of either species fed) to >90% for kudu, eland and nyala (Table 1). Generally, teff and lucerne were the favoured foods, with 64% of feeding animals consuming these *versus* 11% feeding on Boskos; 24% of animals fed on both food types. More Boskos was consumed by sable, kudu, eland and rhino, while other species, including gemsbok and wildebeest, exclusively ate teff/lucerne (Table 1).

Of the 1,431 animals for which we had individual-level feeding data, footage was clear enough to assess body condition for 1,117. Most were in normal condition (544; 48%) but almost half were in poor condition (499; 45%) and a small number were emaciated (73; 7%). There was a statistically significant association between body condition and whether the individual fed or not, with animals in poorer condition more likely to feed (Chi square test for association: $\chi^2 = 29.500$; d.f = 2; P < 0.001 Fig. 4a). Although there were some differences for different species, the same basic pattern was observed for eland, kudu and sable (Fig 4b-d) suggesting this was not driven by species-condition interactions in the dominant species at feeding stations.

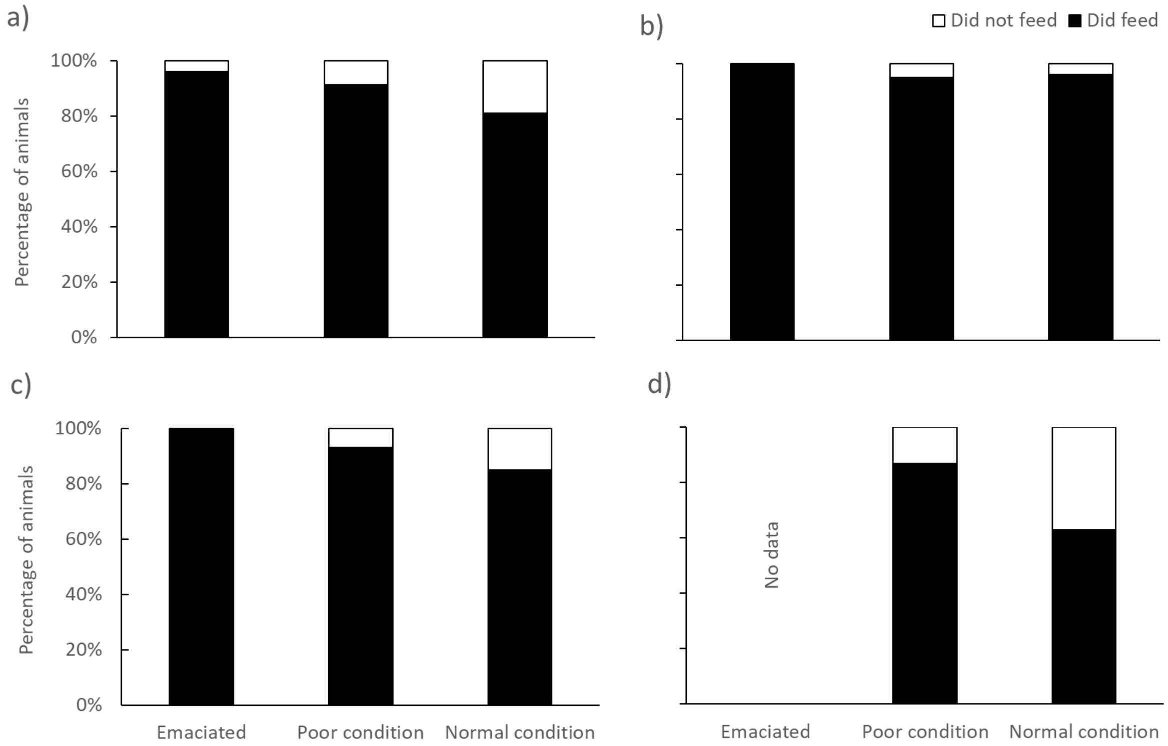

Figure 4 Feeding rates of animals in relation to their body condition for: (a) all individual regardless of species followed by the three species with most body condition data; (b) eland, (C) kudu and (d) sable.

Intraspecific aggression was comparatively rare overall, occurring in 52 of 315 (17%) group visits that involved ≥2 individuals (i.e. when potential intraspecific aggression was possible). Intraspecific aggression was highest for sable (40% of multi-individual visits) and eland (27% of multi-individual visits). Aggression rates were <10% for kudu and wildebeest, and absent for all other species. There were very few interspecific encounters (n = 6 from 490 overall visits; 1.2%) and interspecific aggression was not observed.

Discussion

Overall, feeding stations were well used, with ungulates present for about 25% of the monitored duration. It is not surprising that supplemental food utilisation was unequal between species. However, it is notable that over-represented species (when compared to overall reserve composition) were larger species (eland, kudu, sable and rhino) while under-represented or absent species included smaller species such as impala, blesbok, steenbok (*Raphicerus campestris*) and common duiker (*Sylvicapra grimmia*). Moreover, it was notable that sable, kudu and eland often rested at feeding stations, especially overnight. This could partly be due to a shift in activity budget from foraging to resting (as seen previously in eland in ex-situ environments by Hejcmanová et al. (2013), but it could also be that food resources were being monopolised and guarded by these species. This has been seen previously in multiple sites in North America and Europe (Murray et al., 2016 and references therein). A greater number of lower-intensity feeding stations might reduce exclusion of smaller or less-dominant species (Milner et al., 2014). Allowing food to run out before restocking at random times might also be effective, as seen for avian scavengers (Arrondo et al., 2015). Such measures would also decrease prolonged aggregation at feeding stations, and thus reduce potential pathogen transmission (Thompson et al., 2008; Sorensen et al., 2014) and aggression (as in red deer *Cervus elaphus* (Putman and Staines, 2004)).

It was interesting to observe the high use of feeding stations by browsers, including eland and kudu, relative to grazers such as wildebeest and zebra (classifications per Abraham et al., 2019). This might indicate browsers are more vulnerable to drought than often thought (e.g. McNaughton and Georgiadis 1986; Walker et al., 1987; Duncan *et al.,* 2012) or simply reflect these large species using, and being able to dominate, easily-available food resources. The absence of species associated with natural water courses (waterbuck, reedbuck, and mountain reedbuck) suggests that placement of feeding stations needs careful consideration. It may useful to ensure stations are easily accessible to all species by considering underlying species distributions and species-habitat associations rather than being sited (as here) near to water-holding artificial pans.

Intraspecific aggression was highly variable. It was not directly linked to group size (blesbok and wildebeest had the highest average and highest maximum group sizes, respectively, but no or minimal aggression) and is more likely to reflect species-specific group dynamics and hierarchical structures, as seen previously for eland (Vymyslická et al., 2015). It remains unclear whether levels of aggression seen for eland and sable are reflective of species norms, either in general or in times of food shortage, or amplified at feeding stations. For example, increased aggression in rhino was observed not only during supplemental feeding but also when natural food resources were low (Cinková *et al.,* 2017). This would be an interesting area for future research. It should also be noted that there was a relatively high density of feeding stations (n = 13) relative to the size of the reserve (47 km^2), and this might also have reduced inter-species encounters, and both intra- and inter-specific aggression.

Seasonal weight loss in wild ungulates can be up to 30% of their total body mass (Mitchell *et al.,* 1976). We found that individuals in poor condition were more likely to feed than those in better condition, suggesting that while the supplementary food might be widely used it was especially important for emaciated animals or animals in poor condition. A longer-term study would be needed to establish the effectiveness of supplemental feeding to improve body condition and subsequent fitness and productivity (Murray et al. 2016). Most species use teff/lucerne rather than, or as well as, Boskos. The species that used high levels of Boskos were the four species that were over-represented at feeding station. Moreover, primates, which can often be non-desirable pests, exclusively ate Boskos.

In conclusion, we have shown that: (1) ungulates start utilising supplemental feeding stations very quickly and then use them extensively – this high level of tolerance suggests they are deriving nutritional benefit from it; (2) individuals in poorer condition are more likely to feed; (3) use of feeding stations varies considerably between species and generally larger species seemed to dominate usage; and (4) Boskos was used relatively infrequently except by over-represented / pest species and thus we recommend that while Boskos is widely used *ex-situ*, it should only be considered for use *in-situ* if there is a specific reason to do so.

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Conflict of interest

The authors declare no conflict of interest

Data availability statement

Data are available on the University of Gloucestershire research repository via the following link http://eprints.glos.ac.uk/id/eprint/9978.

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