



Daily visitation patterns and consumption of fleshy fruits of invasive alien plants by wild southern African ungulates

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Received: 21 September 2024 / Accepted: 30 May 2025 / Published online: 20 June 2025
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Abstract

Endozoochorous seed dispersal by ungulates has received increased attention. However, ungulates' daily visitation patterns and fruit consumption of the fleshy fruits of invasive alien plants (IAPs) are poorly documented. Using camera trapping, we documented wild southern African ungulates interactions with three freshly-fruited IAPs, i.e. lantana (*Lantana camara*), bugweed (*Solanum mauritianum*) and cochineal prickly-pear (*Opuntia monacantha*) in KwaZulu-Natal, South Africa. We determined the community of potential ungulate seed dispersers of the IAPs, the daily IAP interaction patterns and quantified relative fruit consumption by ungulates. The level of IAP fruit consumption was significantly different among ungulate species and IAPs and varied with time of day. Giraffe (*Giraffa camelopardalis giraffa*), bushbuck (*Tragelaphus sylvaticus*), impala (*Aepyceros melampus*), nyala (*T. angasii*) and greater kudu (*T. strepsiceros*) showed the highest relative fruit consumption rate, respectively, while the lowest was for blue wildebeest (*Connochaetes taurinus*), and zebra (*Equus quagga*). Impala and greater kudu were recorded interacting with the IAPs from 24h00–06h00, giraffe and nyala from 06h00–12h00, and bushbuck from 18h00–06h00. Overall, *L. camara* was visited mostly during the diurnal-afternoon; however, *O. monacantha* during the nocturnal-morning and *S. mauritianum* during the nocturnal-night. The main ungulates potentially dispersing *L. camara* were giraffe and bushbuck. Impala and greater kudu were the main potential dispersal vectors for *O. monacantha*. Our study showed that camera trapping is useful for determining the interactions between ungulates and IAPs, which is crucial for understanding their potential contribution to the dispersal dynamics of IAPs in African savannas.

Keywords Plant-animal interactions · Zoochory · Seed dispersal · Frugivory · Exotic plants · Bovidae · Suidae · Giraffidae · Equidae · South Africa

Introduction

Animal-mediated seed dispersal involves animal interactions with the plant species whose seeds are to be dispersed for plant colonisation in new habitats (Schupp et al. 1993). Of the diverse pathways that animals disperse seeds, endozoochory is the most popular and well-studied dispersal mechanism (e.g., van Leeuwen et al. 2020). Endozoochorous seed dispersal involves complex successional processes undertaken by the seeds: from animal visitation and fruit consumption, seed transportation via the gut of the animal disperser, to seed deposition at a new location for potential germination of viable seeds. Collectively, these successional stages potentially lead to effective dispersal (Traveset et al. 2007; Campos et al. 2018), consequently influencing plant spatial distributions (Cain et al. 2000; Pellerin et al. 2016), plant demography, and regeneration (Howe and Smallwood

Handling editor: Vera Rduch.

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1982; Baltzinger et al. 2019). Moreover, animal visitation and fruit consumption elucidate the number of seeds an animal can disperse at a given time (Vázquez et al. 2005), and thus can be used for determining interaction strength and effectiveness between fruiting plants and potential dispersers (Schupp et al. 1993; Campos et al. 2018).

In endozoochorous dispersal, frugivores show preferences for fruits based on traits such as fruit type, seed production, plant height, fruit palatability, seed digestibility and nutritional content (e.g. Gosper and Vivian-Smith 2009, 2010), which influences the strength of fruit-frugivore interaction. The mutualistic relationship between fleshy-fruited plants and animal dispersers consists of a nutritional reward from fruit pulp for frugivores and dispersal service by frugivores for the plant (Wilson and Downs 2012; Zungu and Downs 2017).

There is a lack of literature on fleshy-fruited invasive alien plants (IAPs) seed dispersal by wild ungulates, and ungulates are underrated and less explored than birds in terms of dispersal purposes for IAPs (Baltzinger et al. 2020). Although some studies have investigated ungulate species as seed vectors (e.g. Milton and Dean 2001; Shiponeni and Milton 2006), only 32% of the 257 ungulate species have been explored globally and even fewer documented interactions of fleshy fruits of IAPs with ungulates (Baltzinger et al. 2020). Seeds that pass through the gut of ungulates are subjected to longer seed retention, allowing for the regurgitation (Delibes et al. 2019) or defecation of viable seeds for successful germination (e.g. Picard et al. 2016). In the context of IAPs, interactions with ungulates potentially contribute to their invasion (Williams and Ward 2006). Generally, IAPs negatively impact ecosystems and biodiversity, reducing native habitat availability (Traveset and Richardson 2006; Bitani et al. 2020), and influencing native plant species distribution, richness and abundance (Gaertner et al. 2009; Vilà et al. 2011). The IAPs proliferate, expanding their distribution, spread by vertebrate seed dispersers (Baltzinger et al. 2020; Bitani and Downs 2022).

Camera traps are used as a non-invasive indirect technique to monitor frugivorous interactions with ungulates (e.g. Prasad et al. 2010; Campos et al. 2018). They are useful for accurate animal identification and nocturnal activity detection (Rivas-Romero and Soto-Shoender 2015; Ortmann and Johnson 2021). Therefore, they appear relevant for studying ungulate visitation, fruit consumption and daily activity patterns with fleshy-fruited IAPs.

We documented visitation patterns, fruit consumption frequencies and circadian interaction patterns between wild southern African ungulates and three IAPs: lantana (*Lantana camara*), bugweed (*Solanum mauritianum*), and cochineal prickly-pear (*Opuntia monacantha*). Our main objectives were to (1) determine the community of potential ungulate

seed dispersers of these IAPs, (2) quantify relative fruit consumption among ungulates, and (3) highlight specific daily IAP-ungulate interaction patterns. As IAP fleshy fruits are available during a period when other fruits are absent, we hypothesised that a diverse range of wild southern African ungulates would rely on this transient resource, and thus visit and ingest fleshy-fruited IAPs. Moreover, the ungulate species occurring in our study sites differ in their feeding types (Hofmann 1989). Concentrate selectors (e.g. giraffe (*Giraffa camelopardalis giraffa*), bushbuck (*Tragelaphus sylvaticus*), greater kudu (*Tragelaphus strepsiceros*) consume rich food items (e.g. fruits, buds), whereas grass and roughage eaters (e.g. blue wildebeest (*Connochaetes taurinus*)) mainly feed on short grasses. Intermediate mixed feeders (e.g. impala (*Aepyceros melampus*)) lie in between. We thus hypothesised different visitation patterns and fruit consumption between IAPs and ungulates.

Materials and methods

We conducted our study on three private game properties in KwaZulu-Natal Province, South Africa: Fountainhill Estate (FHE), Zingela Safari and Water Company (Zingela) and Nkonka Lodge-Nyala Pans (NLNP) (Supplementary information Fig. S1). At least 16 ungulate species occur across these sites; 15 in FHE, 11 in Zingela, and nine in NLNP (Supplementary information Table S1). The FHE (ca. 2330 ha; 29°29'34.25"S, 30°30'55.97"E) is a multi-purpose land-use habitat including a 1600 ha nature conservation reserve and a 730 ha commercial farm. Zingela (ca. ~1200 ha, 28°43'24.74"S, 30°03'55.80"E) forms part of a mosaic habitat of protected, semi-protected and unprotected communal areas with free-ranging wildlife in the outskirts of Weenen and Colenso. Nkonka Lodge (ca. 3000 ha; 30°00'05.91"S, 30°11'12.20"E) and Nyala Pans (ca. 3000 ha; 29°59'27.96"S, 30°09'46.80"E) are adjacent to another in the Umkomaas River Valley, both practising similar free-ranging game and cattle ranching, animals moving freely and rotating from site to site. Therefore, both sites were grouped as a single site, NLNP (29°59'43.84"S, 30°11'062"E).

We studied three IAPs, lantana, bugweed and cochineal prickly-pear, all category 1b invasive species in South Africa. This means they are detrimental to the environment and their management and control are compulsory (National Environmental Management: Biodiversity Act, Act 10 of 2004) (NEM: BA, Act 10 of 2004) (Supplementary information Table S2) as they are increasing in distribution. Lantana was generally found in dense populations, forming thicket clusters within savanna and thicket habitats in FHE and NLNP, but more sparsely distributed in Zingela (LM

and CTD pers. obs.). It is partially managed through chemical control in FHE and Zingela, but not in NLNP. Bugweed was sparsely distributed across all three sites (LM and CTD pers. obs.), and not managed or controlled. Cochineal prickly-pear only occurred in Zingela, on severely eroded soils, and the largest population is found in degraded woodland habitats (LM and CTD pers. obs.).

Using camera trapping, we determined animal interactions (visitation and fruit consumption) and daily interaction patterns during IAPs' fruiting seasons. Each camera trap station was determined by the presence of ripe IAPs' fruits, and each camera trap station was considered as an independent observational point. We established 13 camera traps (Moultrie M880i, LLC, Alabaster, USA), four at FHE and Zingela, and five at NLNP, for 21 consecutive days per camera trap station, running 24 h/day. The number of camera traps in each study site was determined by the presence of IAPs and the accessibility of infested areas for camera trap deployment. Before camera trap installation started, we conducted a field assessment survey to identify IAPs invaded areas through direct observations while driving and walking active wildlife trail transects. Each camera trap station selected was distant from at least 200 m from the previous one, depending on the size of IAPs' fruiting stands. Camera traps were placed to focus on IAPs' fruiting stands near active wildlife trails (i.e., the presence of ungulate dung). Camera traps were installed 1–3 m away from the fruiting IAPs, and between 2 and 6 m in height to accommodate varying body heights of ungulates in the area. Camera traps were set to focus solely on fruits hanging on shrubs and trees, and neglected those on the ground. Sampling effort varied with IAP and study site because of the number of camera traps available and IAP presence in each site. This prevented the analysis of the site effect; data analyses were thus presented collectively per IAPs and ungulates across all sites. We used digital images captured by the camera traps to distinguish independent visitation events (e.g., Campos et al. 2018). We excluded by-catch of other vertebrates and focused on processing only wild southern African ungulates. To eliminate data duplication, we used the following parameters to differentiate independent events: consecutive images of different species, non-consecutive images of individuals of the same species (Campos et al. 2018), and consecutive images of individuals of the same species taken 2 min. apart (Prasad et al. 2010). Some individuals were more easily identifiable by their pelage patterns. Our IAPs are multi-seeded and have large fruit production (Bitani et al. 2020). So, the total number of seeds consumed could not be quantified using camera trapping, as ungulates were captured feeding directly on the fruiting IAP shrubs. To quantify ungulate-IAP interaction as a determinant for seed dispersal, we considered the total number

of visitations and the relative fruit consumption proportion (defined as the ratio of the number of visitations with fruit consumption by an ungulate species to the total number of visitations with fruit consumption by all ungulate species during the camera trap survey).

A Poisson Generalised Linear Model (GLM) for count data was used to understand the preference of feeding or not feeding, described as visitation with (= 1) and without (= 0) fruit consumption, as a function of ungulate species, IAP species and period of the day as predictors. The Poisson GLM was conducted using a loglinear function for the Wald chi-square statistics (χ^2). If there were any significant differences, post hoc Tukey (HSD) tests were used to investigate significant differences and pairwise t-tests using One-way ANOVA. Diurnal interactions were characterised by visitations occurring from 06:00–11:59 (diurnal-morning written as D.am) to 12:00–17:59 (diurnal-afternoon written as D.pm), and nocturnal interactions from 18:00–23:59 (nocturnal-night written as N.pm) to 00:00–05:59 (nocturnal-morning written as N.am). We also tested the correlation between the total number of visitations and the relative fruit consumption percentage to understand ungulate-IAP interactions. All assumptions for statistical analyses were met. They were performed with IBM SPSS Statistics (SPSS Inc, version 28, USA). Temporal patterns (mean $\pm$ standard deviation (SD)) of the captured images determined daily ungulate-IAP interaction patterns during night and day using Oriana 4.0 software (Kovach Computing System, UK).

Results

Ungulate visitation pattern and fruit consumption

Camera traps captured 472 independent animal interaction events among 1277 images captured during the 252 camera trap days (one camera trap malfunctioned in FHE). Batteries of some cameras were depleted before 21 days; however, all camera traps captured images for more than 15 days. Eight ungulate species visited IAPs' fruits shown by a significant difference in their visitation rates (GLM, $\chi^2=214.03$; $df=7$; $p=0.001$) (Fig. 1a, Supplementary information Fig. S2).

There was a significant difference in fruit consumption events among ungulates (GLM, $\chi^2=66.721$; $df=6$; $p=0.001$); only the common warthog (*Phacochoerus africanus*) did not show evidence of IAP fruit consumption. Of the seven ungulate species observed foraging IAPs fleshy-fruits, giraffe (53.0%), bushbuck (16.1%), impala (11.4%), nyala (*Tragelaphus angasii*) (8.7%) and greater kudu (8.7%) showed the highest relative fruit consumption rate, and the lowest for blue wildebeest (1.3%) and zebra (*Equus quagga*) (1.3%) throughout the study (Fig. 1b).

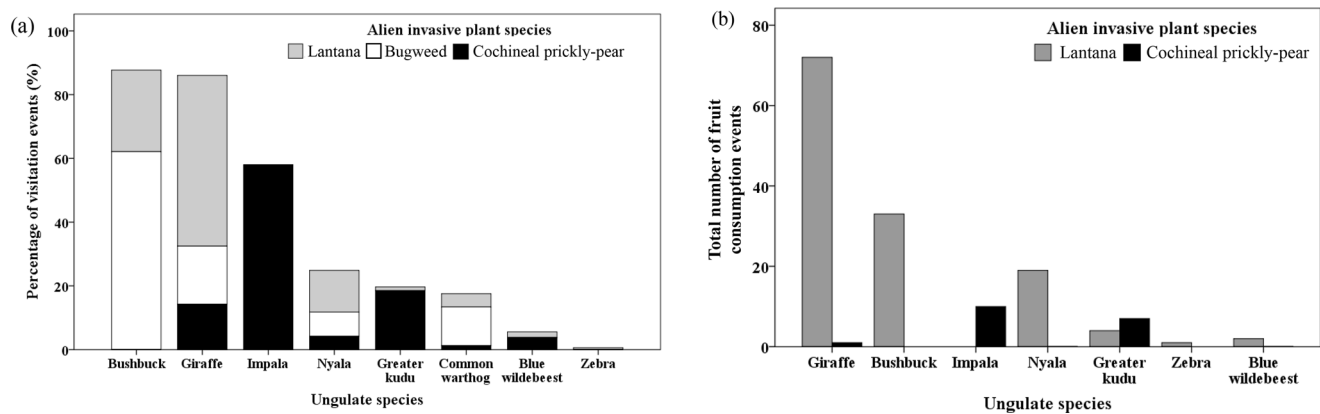


Fig. 1 Summary of “a” relative percentage of independent visitation events of a guild of ungulate species (bushbuck (*Tragelaphus sylvaticus*), giraffe (*Giraffa camelopardalis giraffa*), Impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), greater kudu (*Tragelaphus strepsiceros*), common warthog (*Phacochoerus africanus*), blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*)) observed/

captured visiting and ingesting alien invasive lantana (*Lantana camara*), bugweed (*Solanum mauritianum*) and cochineal prickly-pear (*Opuntia monacantha*) in the present study, and “b” total number of fruit consumption events for each ungulate species that ingested one of the two following invasive alien plants (Lantana and Cochineal prickly-pear) in the present study

Overall, all three IAPs were visited by ungulates and presented a significant difference in total number of visitations (GLM, $\chi^2=85.53$; $df=2$; $p=0.001$); but only lantana and cochineal prickly-pear fleshy fruits were ingested by ungulates (Fig. 1b). There were significant differences in the total number of fruit consumption events for each IAP (GLM, $\chi^2=62.345$; $df=1$; $p=0.001$). Although cochineal prickly-pear ($n=238$) attracted a higher number of visitations than lantana ($n=168$) and bugweed ($n=66$); lantana fleshy fruits ($n=131$) were ingested more frequently than cochineal prickly-pear ($n=18$) (Fig. 1). Lantana was visited by seven ungulate species; however, its fruits were mostly ingested by giraffe, bushbuck and nyala, respectively (Fig. 1). Of the six ungulate species observed visiting cochineal prickly-pear, impala, greater kudu, and giraffe showed the highest evidence of fruit consumption, respectively (Fig. 1). Bugweed was mostly visited by bushbuck and giraffe, respectively (Fig. 1a); but never observed consumed during the camera trap survey by any ungulate species (Fig. 1b). There was a significantly strong positive correlation between the total number of visitations and the relative fruit consumption percentage ($r=0.748$; $p=0.033$).

Circadian interaction patterns

There was no significant difference in the total number of visitations at different periods of the day (GLM, $\chi^2=3.261$; $df=3$; $p=0.353$); however, a significant difference was observed for total fruit consumption events at different periods of the day (GLM, $\chi^2=105.901$; $df=6$; $p=0.001$), with D.pm and D.am receiving the highest fruit consumption rate, respectively. The main differences were observed between the following pairs: N.am-D.am ($p=0.001$),

N.am-D.pm ($p=0.001$), D.am-N.pm ($p=0.004$) and D.pm-N.pm ($p=0.004$). There was no difference in the total number of diurnal and nocturnal visitation rates (GLM, $\chi^2=1.025$; $df=1$; $p=0.311$); however, a significant difference was observed for the fruit consumption rates (GLM, $\chi^2=50.286$; $df=1$; $p=0.001$). Ungulates recorded visiting and ingesting IAP fruits exhibited differences in their daily temporal interaction patterns (mean $\pm$ SD in hours). Impala ($02:46 \pm 4.87$ h) and greater kudu ($02:39 \pm 4.65$ h) were recorded interacting with IAPs during N.am, giraffe ($11:23 \pm 4.62$ h) during D.am, nyala ($12:21 \pm 5.33$ h) during D.pm, and bushbuck ($21:14 \pm 4.23$ h) during D.pm (Fig. 2). There was no overlap in daily interaction patterns of ungulates with IAPs. Overall, ungulates visited and ingested lantana mostly during D.pm ($12:08 \pm 0.67$ h), cochineal prickly-pear during N.am ($03:46 \pm 0.52$ h) and bugweed during N.pm ($18:59 \pm 0.63$ h) (Fig. 3).

Discussion

Animal visitation and fruit consumption are important to quantitatively determine animal efficiency as seed dispersers (Schupp et al. 1993). We report here on animal visitation, fruit consumption and daily interaction patterns of wild southern African ungulates with fleshy-fruited IAPs using camera trapping. Our survey showed a diversity of ungulates visiting and ingesting IAP fruits, therefore, potential seed dispersers. We identified eight ungulates (giraffe, impala, nyala, zebra, blue wildebeest, greater kudu, common warthog and bushbuck) visiting IAPs, among which only common warthogs did not ingest the fruits during the survey. However, warthogs are known to forage fallen fruits

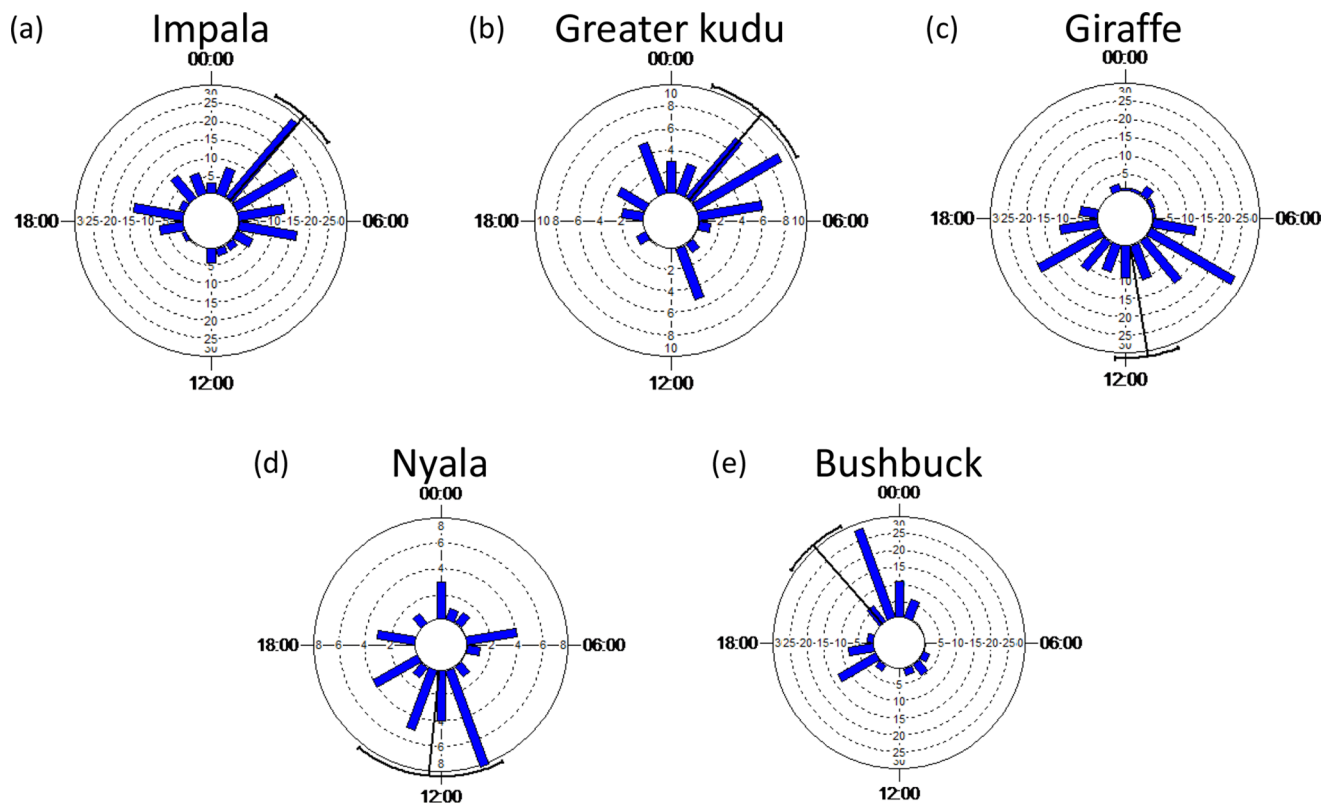


Fig. 2 Circadian interaction patterns of the top five potential ungulate dispersers (“a” impala (*Aepyceros melampus*), “b” greater kudu (*Tragelaphus strepsiceros*), “c” giraffe (*Giraffa camelopardalis giraffa*), “d” nyala (*Tragelaphus angasii*) and “e” bushbuck (*Tragelaphus sylvaticus*)) recorded visiting invasive alien plant species (all

three plants combined) in the present study. (Note: Bars of histogram plot for 24-h activity indicate the relative frequency of records in each hour, a longer bar meaning greater clustering of the data around that hour)

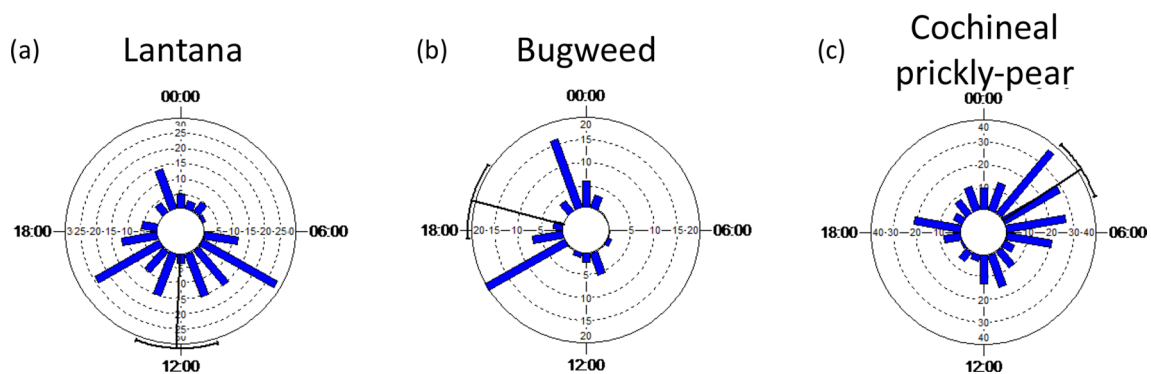


Fig. 3 Circadian interaction patterns of ungulates visiting each fruiting invasive alien plants (“a” lantana (*Lantana camara*), “b” bugweed (*Solanum mauritianum*) and “c” cochineal prickly-pear (*Opuntia monacantha*)) in KwaZulu-Natal, South Africa. (Note: Bars of histogram

plots for 24-h activity indicate relative frequency of records in each hour, and a longer bar means greater clustering of the data around that hour)

underneath fruiting plants (Edossa et al. 2021), and our camera traps were focused on hanging fruits of each IAP, and not on the ground and potential fruits lying on the ground.

Evidently, ungulate species with higher visitations had more opportunities for IAP fruit consumption, underlined by a strong positive correlation between the total number of visitations and relative fruit consumption percentage.

Giraffe, bushbuck, impala, greater kudu, and nyala had the strongest interactions with IAPs, suggesting they could be the most effective potential seed dispersers for the studied IAPs. Despite the lack of literature on fleshy-fruited IAP seed dispersal by wild ungulates, Grünwald et al. (2010) and Prasad et al. (2010) reported on the dispersal effectiveness by wild ungulates. Ungulates are underrated and less

explored than birds in terms of dispersal purposes for IAPs (Baltzinger et al. 2020). Therefore, factors such as long seed retention time (Picard et al. 2015) and large home ranges (Pellerin et al. 2016) allow ungulates to successfully disperse seeds of IAPs over long distances.

The total number of IAP fruits consumed was significantly different for the different ungulates and IAPs as hypothesised. According to Vázquez et al. (2005), visitation frequencies may sometimes be used as an estimator of fruit removal when fruit consumption is difficult to validate. However, this is not always the case, as some visitors do not consume fruits directly from the IAP (Howe 1986), as observed for common warthogs in our study, amplifying the importance of differentiating between visitation with and without fruit consumption directly from the IAP.

Although we found higher visitations to cochineal prickly-pear than to lantana; fruits of lantana were more frequently ingested. Seven ungulate species visited lantana, but its fruits were mostly ingested by giraffe, bushbuck and nyala. We expected a lower fruit consumption of lantana by ungulates than any other IAPs since it is reported as toxic to mammals, causing organ failure and eventually death (Botha and Penrith 2009). According to Launchbaugh et al. (2001), ungulates develop innate and learned feeding strategies to cope with plant toxic chemicals, eventually tolerating the toxins and ingesting more of the plant.

Additionally, we showed that the total number of IAP fruits consumed did not depend on the time of the day, but ungulate species visited the fruiting IAPs at different times of day. We focused on the top five ungulates observed ingesting IAPs, as their visitation had higher probabilities for fruit consumption. Impala and greater kudu were recorded interacting with IAPs during nocturnal-morning, giraffe and nyala during diurnal-morning, and bushbuck during nocturnal-night periods. Though not tested here, plant-animal interactions are determined by a range of factors (Ensing et al. 2014; Owen-Smith and Goodall 2014). Additionally, ungulates prioritise periods of optimal foraging, therefore determining their interaction patterns with plants (Khan et al. 2023). Our study suggests minimal competition for IAPs as a food source among ungulates, as we found no overlap in daily interaction patterns between ungulate species and IAPs. Lantana was visited mostly during the diurnal-afternoon; cochineal prickly-pear during the nocturnal-morning and nocturnal-night period for bugweed. Visitation and fruit consumption patterns of the IAPs were determined by the feeding behaviour of the dominant ungulate visiting the plant.

In conclusion, camera trapping enabled the identification of ungulates visiting and ingesting IAPs during night and day. However, we failed to assess the number of IAP fruits ingested, which is necessary to establish each ungulate's seed dispersal effectiveness (Fedriani et al. 2024). Our study made an important contribution by tackling the community of ungulates as

a whole, notably showing resource partitioning among the different ungulates feeding upon IAP fleshy fruits. Generally considered dispersed by birds and primates, the present study unveiled the hidden face of IAP dispersal by wild ungulates, which are long-distance seed dispersers. Understanding their potential contribution to the dispersal dynamics of IAPs in African savannas is thus crucial. It remains to be studied whether ungulates prefer IAPs to native plants or whether this is linked to a staggered and non-overlapping fruiting phenology.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42991-025-00505-y>.

Acknowledgements We are most grateful to the management of all the study sites (Fountainhill Estate, Zingela and Nkonka Lodge-Nyala Pans) for allowing us to conduct our research on their properties. We thank Dr N. Bitani and Dr M. Maseko for their valuable insights and encouragement. We would also like to thank L. Tsoananyane, B. Mthethwa, M. Dladla, and N. Mtshali for assisting with the camera-trapping fieldwork. This project was funded by the National Research Foundation (NRF, ZA) through the Centre for Invasive Biology (CIB) and the NRF Chair (Grant 98404). We also thank the University of KwaZulu-Natal (ZA) for funding and appreciate vehicle support provided by the Ford Wildlife Foundation (ZA). We thank the reviewers whose comments improved our manuscript.

Author contributions All authors conceptualised the study. CTD sought funding. LSM collected and analysed data. LSM drafted the manuscript. MMZ, CB and CTD edited this.

Funding Open access funding provided by University of KwaZulu-Natal.

Data availability The data belong to the University of KwaZulu-Natal and are available from the corresponding author on reasonable request.

Declarations

Ethical approval Not applicable as camera traps were used to collect data.

Conflict of interest The authors declare no competing interests.

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