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Wild ungulate foraging suppresses growth of invasive parthenium weed

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The invasive weed *Parthenium hysterophorus* has severely disrupted ecosystems worldwide, driven by its persistent seed bank and phytotoxic compounds that suppress surrounding vegetation and negatively impact herbivorous mammals. It is widely assumed that wild ungulates avoid parthenium weed-dominated areas due to its presumed unpalatability and toxicity, but direct evidence is limited. We experimentally tested whether ungulates in an African savanna actively forage on parthenium weed by contrasting herbivore foraging in mechanically cleared and controlled areas using exclosures in parthenium-invaded areas. We also assessed whether reduction in body condition scores was associated with foraging on parthenium weed, and whether herbivory suppresses parthenium weed regrowth. Our experimental results show that ungulates foraged on parthenium rosettes without apparent negative impacts on body condition. Notably, herbivore activity significantly reduced parthenium cover in cleared areas. These findings reveal a previously undocumented potential for leveraging wild ungulate herbivory as a biocontrol mechanism for managing parthenium weed invasions.

1. Introduction

Alien invasive plant species pose a substantial threat to the ecological integrity of open canopy and savanna systems by altering vegetation structure, nutrient cycling and fire regimes [1–3]. Their establishment often leads to the displacement of native grasses and woody plants, reducing biodiversity and undermining the resilience of these ecosystems [4]. Invasive species can also disrupt key ecological processes, such as herbivore foraging dynamics and predator–prey interactions, ultimately affecting both wildlife populations and human livelihoods dependent on savanna resources [5]. Understanding and mitigating the impacts of invasive plants is, therefore, critical for the conservation and sustainable management of African savanna landscapes.

Invasive plants can alter herbivore foraging patterns by outcompeting or replacing native food sources. Herbivores often rely on visual and olfactory cues to select foraging sites, associating high biomass with nutritional quality [6]. When invasive plants form dense stands, such cues may lead herbivores to selectively use these invaded areas. However, if the invasive forage lacks nutrients or contains detrimental secondary compounds, there may be negative effects for the herbivore, potentially causing ecological traps [7,8].

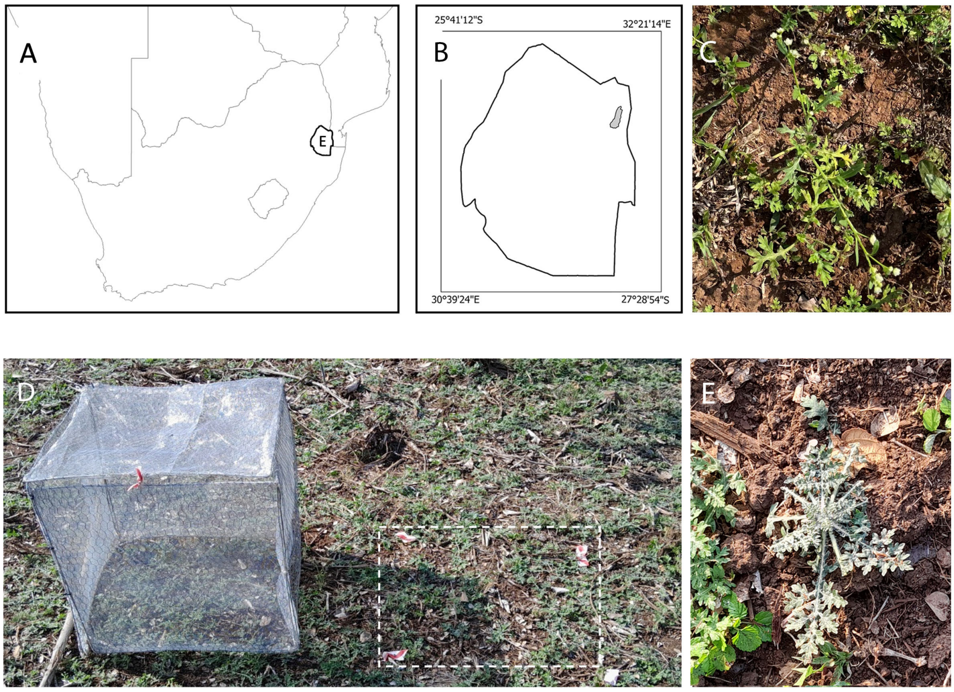

Figure 1. Map of Southern Africa (A) with E indicating Eswatini, enlarged in (B) with Mlawula Nature Reserve shown in grey, where the study was conducted. An adult parthenium weed (C), experimental set-up showing a cage (left) and an open treatment highlighted by white dashed line (right) (D), and herbivory damage on a parthenium rosette (E).

Parthenium hysterophorus L. (Asteraceae), commonly referred to as 'parthenium weed', is an infamous weed [9] and one of Earth's most destructive invasive plants [10]. Native to the American tropics, it has successfully invaded much of Asia, Africa and Oceania. Parthenium weed primarily invades areas that have been disturbed or overgrazed [2], where it forms dense monocultures and outcompetes native flora, dramatically altering ecosystem structure and function. Parthenium weed has far-reaching detrimental ecological and socioeconomic impacts [11–13] and adverse effects on agricultural productivity and livestock health [14]. Its ability to invade and dominate vegetative cover in grasslands is a function of its life history [15], with its ability to germinate year-round [4] and maintain a long-lived seed bank [15]. Its potent secondary compounds are known to pose risks to mammals; in livestock, ingestion has been linked to toxicity, reduced productivity and, in severe cases, death [16,17].

Despite widespread concern about the threat parthenium weed presents to wildlife, little research has examined its impact on wild ungulates. It is commonly believed that wild mammalian herbivores avoid areas dominated by parthenium weed due to its presumed unpalatability and toxicity [2,18,19], which limits available forage; therefore, if parthenium weed is detrimental to herbivores, negative health consequences should be observable. Alternatively, while herbivores may facilitate aspects of exotic plant invasions [20], it may be that herbivory impedes parthenium growth, much like herbivory limiting liana growth in East Africa [21]. To test these assumptions and gain a better understanding of wild ungulate responses to parthenium weed, we addressed the following questions: (i) do ungulates alter their activity in areas with high parthenium weed density? (ii) Do the most common species frequenting these areas have relatively poorer body conditions? (iii) Does herbivory limit the growth of parthenium weed? We predicted that (i) ungulates would avoid areas dominated by parthenium weed, (ii) individuals in these areas would exhibit signs of poor body condition or nutritional stress (e.g. [1]) signalling evidence for an ecological trap and (iii) herbivory would have minimal impact on the weed's growth or abundance. Alternatively, if ungulates do forage on and suppress parthenium weed, this may be an approach to controlling parthenium weed within African savannas [22,23].

2. Methods

(a) Study area

We conducted our research in Mlawula Nature Reserve (26.180° S, 31.998° E), a 165 km^2 protected area, located in the lowveld of northeastern Eswatini (figure 1). The reserve occurs in the lowland savanna biome and includes part of the Maputaland-Pondoland-Albany biodiversity hotspot [24,25]. The dominant overstory trees in the reserve include *Senegalia (Acacia) nigrescens* and *Sclerocarya birrea* subsp. *caffra*. The shrub layer, dominated by *Dichrostachys cinerea* and *Ziziphus mucronate*, can be dense (>40% coverage) [26,27] and ground cover can be sparse (<30% coverage), with *Themeda triandra* and *Panicum maximum*as the most common grasses. Common ungulate herbivores at this reserve include impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), common duiker (*Sylvicapra grimmia*), greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus quagga burchellii*) and Cape bushbuck (*Tragelaphus sylvaticus*). The reserve receives an average of 500–750 mm of rainfall, primarily between October and March [24].

To reduce encroaching shrubs and increase the visibility of game species, the reserve undertook mechanical clearing efforts from November 2023 until March 2024. Using a roller-chopper, an area roughly 4 km by 150 m wide was cleared (approx. 60

Table 1. Pairwise comparisons of ground cover categories in cleared and uncleared plots. The table includes estimates of cover, *z*-scores and Holm-adjusted *p*-values.

cover category	cleared	uncleared	*z*-score	*p*
bare ground	0.59	0.38	1.45	0.334
forbes	0.08	0.13	−1.59	0.334
grasses	0.14	0.40	−2.19	0.113
parthenium	0.08	0.01	3.07	0.010
woody	0.10	0.08	1.08	0.334

ha). This activity resulted in areas with negligible shrub cover and highly disturbed ground cover. At the beginning of May 2024, the ground cover of the roller-chopped area appeared to be dominated by parthenium weed and woody debris.

(b) Ungulate activity

To test if there were differences in ungulate activity and body condition within areas of extensive parthenium weed coverage, we established 11 sites within the reserve: five sites in the recently disturbed parthenium weed-abundant areas (parthenium coverage > 80%) and six sites in adjacent areas (500–1500 m from the cleared area) that spanned a range of ground cover (20–60%) and were relatively parthenium weed free. At each site, we installed three game cameras, with two cameras (Moultrie, M-880, Birmingham, Alabama) programmed to capture photos and one to record videos (Browning Dark Ops, Morgan, Utah). We installed cameras on trees at 50 cm height, facing game trails. We removed any small woody and herbaceous vegetation in the line of sight of the cameras as needed [28] and programmed cameras to record 30 s videos or take a burst of three photos every minute when motion was detected.

We compiled detection data from all camera traps and processed them using the camtrapR package [29]. To reduce the chances of counting individuals multiple times, we only retained detections where there were at least 15 min separating them from another detection of same species on the same plot [30]. To analyse treatment effects, we focused on all herbivores combined as well as individual herbivore species with >25 detections. We modelled detection counts using generalized linear models with a quasi-Poisson distribution to account for overdispersion. We included treatment (cleared site versus uncleared site) as a fixed effect and added the log of camera days as an offset to account for variation in survey effort. We visualized predicted responses of herbivores with statistically significant responses.

(c) Body condition

To quantify the body condition of the two most common ungulates (impala and nyala), we randomly selected 10 independent detections of each species from each site. In cases where multiple animals occurred in the detection, we scored the animal closest to the camera. If the randomly selected detection was not scorable (e.g. too far from the camera), we move forward in time until the next scorable detection of that species was found. We ranked ungulates using the visual body condition score described by Riney [31]. Animals were given a score of 1 (poor), 2 (fair) to 3 (good) based on an examination of ribs and pelvic region. We calculated average scores and the proportion of poor and fair individuals in each treatment. Additionally, if no individuals were scored as poor, we compared the proportion of fair with good individuals between areas (cleared, uncleared) using a generalized linear mixed model (GLMM) with a binary distribution and area type (cleared, uncleared) as a fixed effect and site as a random effect.

(d) Ground cover

To quantify the difference in the ground cover between clear and unclear sites, we randomly placed a 1 m^2 quadrat within the detection zone of each camera set on video mode. We classified the per cent ground cover in each quadrat into five categories: bare ground, grasses, forbs, woody vegetation and parthenium weed.

We analysed how proportional ground cover, including parthenium weed, differed between cleared and uncleared sites by modelling variation in the cover of each vegetation category (bare ground, grasses, forbs, woody vegetation and parthenium weed). To avoid violating the assumption of independence among compositional cover types, we fit separate GLMMs for each category using a beta distribution in the glmmTMB package [32] in R [33]. Each model included treatment group (cleared versus uncleared) as a fixed effect and plot as a random effect. We used an ANOVA to evaluate treatment effects within each category and estimated marginal means with the emmeans package [34]. We then conducted pairwise comparisons between treatments within each vegetation category, and *p*-values were adjusted for multiple comparisons using the Holm method to control for family-wise error across the set of tests. Finally, we visualized the predicted responses and 95% confidence intervals for each ground cover category and considered pairwise differences statistically significant when $p < 0.05$.

(e) Parthenium exclusion plots

To test if ungulates could influence the growth of parthenium weed rosettes, we used a before–after, control–impact experimental design. We identified an additional seven sites with extensive parthenium weed growth in areas that had been disturbed,

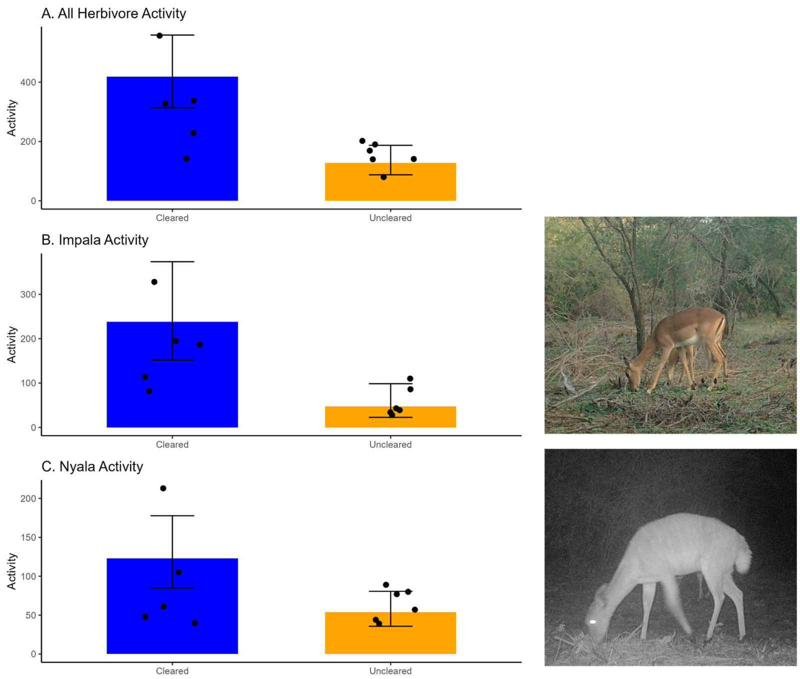

Figure 2. Predicted herbivore activity in cleared and uncleared plots based on quasi-Poisson generalized linear models. Bars represent model-estimated mean detections per plot for (A) all herbivores combined, (B) impala and (C) nyala, adjusted for sampling effort (log-transformed camera days included as an offset). Error bars show 95% confidence intervals. Black dots represent raw observed detection counts per plot.

near the sites where ungulate activity was monitored. At each site, we identified two 60 × 60 cm plots with roughly comparable amounts of parthenium weed and bare ground. For each pair, we randomly selected a treatment plot to receive a wired cage (60 × 60 × 60 cm cube wrapped in 10 mm mesh wire), while the paired plot was left open to herbivores (control). While the cages were also likely to exclude more cryptic herbivores (e.g. birds and rodents), our cameras, observations and detailed inspections of herbivory on the plants did not indicate these smaller herbivores were foraging on the sites with extensive parthenium weed. We installed the exclosures on 25 May 2024 and removed them after six weeks (6 July 2024). To assess the cover and foraging activity on parthenium weed, we took a standardized image of each plot using an iPhone 13 Mini® at a height of 110 cm perpendicular to the ground when exclosures were put up (May) and then again after six weeks (July).

We used the images to quantify parthenium weed cover in each cage or plot by first cropping the image into equally sized squares using Adobe Photoshop (v. 6.0) and removing vegetation that was not parthenium weed using the eraser tool. Next, we used the colour threshold in ImageJ (v. 1.54, [35]) to adjust the hue and brightness levels (range: 40–50) and to isolate green plant material, which represented parthenium weed cover. Then we converted each image to a binary layer (black/white) to estimate parthenium weed cover. Additionally, we imported the binary image into DotDotGoose (v. 1.7.0, accessed 2024 [36]) to estimate the proportion of plants that showed evidence of foraging. Using the original images in DotDotGoose, we were able to count the number of rosettes and adults that showed clear evidence of herbivory (electronic supplementary material, figure S1).

To evaluate changes in the amount of cover and the portion of parthenium weed eaten following the exclusion experiment, we used a paired repeated measures design. We compared treatment and control plots both before and after the exclusion using a paired Hedges' g to estimate standardized effect sizes. We used Hedges' g to express the difference between group means in units of pooled standard deviations (s.d.), allowing biological interpretation of effect magnitude (e.g. values >0.8 indicate large effects; [37]). An advantage of Hedges' g over non-parametric alternatives (e.g. median differences) is that it captures both the size and consistency of treatment effects by incorporating within-pair variation. This allows a clearer interpretation of how large and reliable the exclusion effects were, beyond central tendency alone [37,38]. We calculated bootstrapped 95% confidence intervals and conducted two-sided permutation t-tests [39,40]. We visualized the raw paired data, effect sizes and bootstrapped confidence intervals using Gardner–Altman estimation plots [38]. All analyses were conducted using https://www.estimationstats.com/#/ and dabestr 3.0 R package [40].

3. Results

We found differences in the per cent cover of parthenium between cleared and uncleared areas (z-score = 3.08, adjusted p = 0.010). No other ground cover category differed significantly between cleared and unclear plots (electronic supplementary material, figure S2). The ground was covered by roughly 8% parthenium (95% CI 4–18%) on cleared site and only 1% in uncleared sites (95% CI 0–3%; table 1, electronic supplementary material, figure S2).

We recorded 2516 independent detections from 10 different ungulates. We modelled the total ungulate and species-level responses to cleared and uncleared areas for all species except red duiker (*Cephalophus natalensis*, n = 21), Burchell's zebra (*Equus quagga burchellii*, n = 12) and bushpig (*Potamochoerus larvatus*, n = 8), which had limited numbers of detections. All ungulates combined and the two most common species, impala and nyala, presented significantly more activity in the cleared plots (table

Table 2. Detections and modelled treatment (cleared, uncleared) effect sizes (β) of each herbivore. We set cleared sites as the reference category with negative score, suggesting less activity on uncleared sites. We also report standard errors (s.e.), test statistics and p-values.

species	detections	β	s.e.	z-score	p
all herbivores	2516	−1.19	0.24	−4.88	<0.001
impala	1246	−1.62	0.44	−3.68	0.005
nyala	853	−0.83	0.28	−2.95	0.016
bushbuck	131	−0.19	0.74	−0.25	0.806
blue wildebeest	125	−3.81	2.81	−1.36	0.208
greater kudu	50	1.56	1.09	1.43	0.185
warthog	39	−1.99	1.04	−1.92	0.087
common duiker	30	0.97	1.17	0.83	0.427

2, figure 2), with 229, 406 and 129% increases, respectively. The body condition scores of both impala (cleared $\bar{x} = 2.74$, 95% CI [2.62–2.86]; uncleared $\bar{x} = 2.75$, 95% CI [2.64–2.68]) and nyala (cleared $\bar{x} = 2.88$, 95% CI [2.79–2.97]; uncleared $\bar{x} = 2.78$, 95% CI [2.78–2.95]) were almost identical between treatments and did not differ statistically (nyala $\beta = -0.12$, $p = 0.835$; impala $\beta = 0.06$, $p = 0.918$). For impala, we scored 25.5% of the population to be in fair condition, and for nyala, we only consider 12.7% of the population to be in fair condition.

When examining ungulate exclosure plots, before the start of the experiment, we found no differences between treatment and control plots for parthenium weed cover (Hedge's $g = -0.26$ [95% CI −1.60, 1.21], $p = 0.637$) and the portion of parthenium eaten (Hedge's g −0.21 [95% CI −1.30, 0.81], $p = 0.806$). However, after six weeks of excluding herbivores, cover of parthenium weed increased within exclosures (Hedge's $g = 1.43$ [95% CI 0.57, 2.54], $p = 0.011$), while the portion eaten declined markedly (−1.95 [95% CI −3.05, −1.09], $p < 0.001$). The decline in herbivory represents a reduction of nearly 2 s.d., while parthenium cover increased by roughly 1.5 s.d. units (figure 3).

4. Discussion

Our study provides empirical evidence that wild ungulate herbivores, specifically impala and nyala, actively forage on parthenium weed in an African savanna. Contrary to expectations of avoidance and potential fitness costs, we found that ungulates were more active in areas with higher parthenium weed densities and that body condition did not differ between animals in areas with high or low abundance of parthenium weed. Most notably, the herbivory appeared to suppress parthenium weed growth, preventing flowering.

Herbivores did not appear to experience any detrimental effects from the parthenium weed. This may be due to the majority of unexcluded plants being juveniles in the rosette stage. Parthenium weed has an aggressive ability to take up nutrients, particularly nitrogen and phosphorus [39], which may mean juvenile rosettes contain higher nutrient concentrations [39,40] and may also have lower concentrations of chemical defences [39–41]. This potential combination of higher nutritional value and reduced toxicity, particularly lower concentrations of parthenin and other sesquiterpene lactones that are known to deter herbivores [42], may make juvenile plants more desirable to ungulates. Moreover, parthenium weed may also be desirable during the dry season, when this study occurred, when there are often limited foraging options and fewer substantive juvenile plants, as secondary metabolites often increase and nutritional composition often decreases due to resource limitation during drier periods [43]. Consequently, ungulates observed in this study may have foraged on juvenile parthenium weed because of its nutritional value and potentially reduced detrimental effects.

One explanation for why impala and nyala foraged on parthenium weed is that they may be in poor condition and have no alternatives due to limited foraging options. However, our data showed little support for this hypothesis. We found no differences in the body condition of ungulates found in areas with more parthenium weed. Moreover, the 25.5% of impala in fair condition was comparable with other studies that have used the same approach to assess body condition [44–46]. The absence of body condition differences could be because the impala and nyala are using physiological or behavioural adaptations to mitigate harmful effects [47,48], such as selective feeding, rumen detoxification, regulating intake over time and building tolerance over time [48]. Furthermore, the absence of poor body condition indicates that we do not have evidence of a trap, but specific experiments to explore fitness and using older parthenium weed could test this concept more explicitly.

The ability to consume toxic plant species could contribute to the suppression of invasive plant populations [21,49]. While herbivores are often implicated in facilitating invasions through seed dispersal and disturbance, evidence suggests that selective browsing on invasive species may reduce their competitive advantage and limit their dominance in certain ecosystems [50]. For example, in East Africa, giraffes were shown to stem the growth of lianas [21]. Furthermore, in North America, white-tailed deer (*Odocoileus virginianus*) selectively browse on several invasive plants, reducing their spread [51,52]. As mammalian herbivores are capable of ingesting/consuming toxic invasive plants, native mammals could act as a potential biocontrol mechanism.

These findings raise important new questions about the ecological interactions between wild ungulates and *P. hysterophorus*. First, there is a need for detailed analyses of the nutritional content and chemical defence profiles of parthenium at different developmental stages to identify precisely what makes juvenile plants palatable in the savanna. Second, it is important to assess

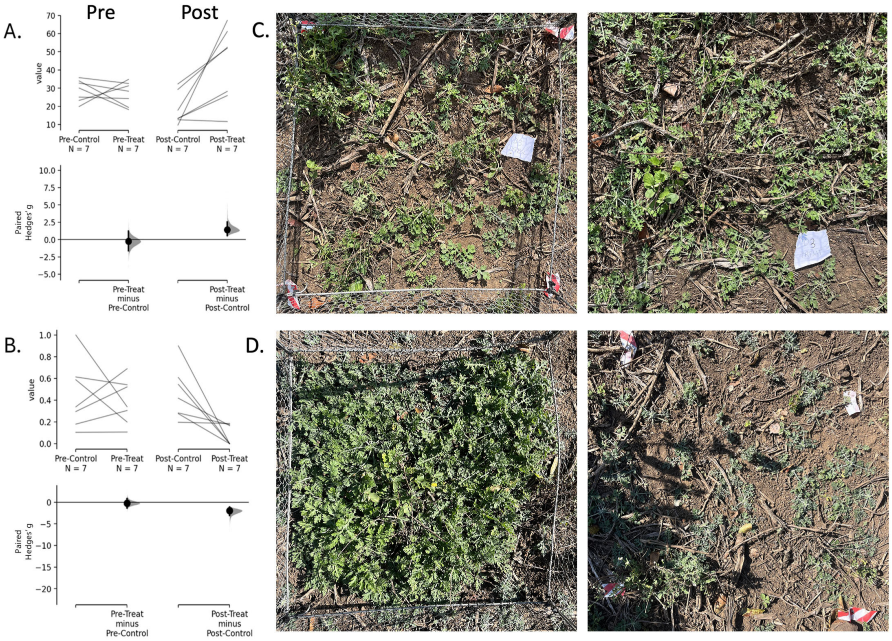

Figure 3. Paired Hedges' *g* for two comparisons between treatments and controls in the % cover (A) and portion of parthenium weed eaten (B) before (Pre) and six weeks after exclusion (Post). The raw data are plotted on the upper axes, and each paired set of observations is connected by a line. On the lower axes, each paired mean difference is plotted as a bootstrap sampling distribution. Mean differences are depicted as dots; 95% confidence intervals are indicated by the ends of the vertical error bars. (C) Images of the experimental units in May for the caged (left) and open (right). (D) Images of the same experimental units photographed in July for caged (left) and open (right) demonstrating that foraging suppressed growth of parthenium weed over the six weeks.

whether this foraging behaviour is specific to mixed (i.e. animals that browse and graze) feeders like impala and nyala or occurs in other herbivores. Finally, the short-term nature of our study limits our ability to assess the long-term population-level effects of herbivory on parthenium. Herbivory alone may not directly translate into reduced seed output or population decline due to the presence of the long-lived, extensive seed bank. Future work should test whether parthenium consumption is an adaptive feeding strategy and whether herbivory prevents plants from reaching reproductive maturity, reducing seed banks, therefore reducing spread.

Ethics. Animal research was conducted under IACUC no. 202011155.

Data accessibility. The datasets supporting this study were uploaded as part of the supplementary material. The dataset includes vegetation survey data, body condition data, and parthenium adult, juvenile and herbivory.

Supplementary material is available online [53].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. Authors' contributions. K.L.G.: conceptualization, data curation, writing—original draft, writing—review and editing; A.T.: data curation, formal analysis, writing—review and editing; E.P.L.: data curation, formal analysis, writing—review and editing; R.J.F. Jr: conceptualization, funding acquisition, supervision, writing—review and editing; S.B.: data curation, formal analysis, supervision, writing—review and editing; L.K.: data curation, supervision, writing—review and editing; M.L.: data curation, formal analysis, writing—review and editing; A.M.: funding acquisition, supervision, writing—review and editing; S.M.W.: funding acquisition, supervision, writing—review and editing; R.M.: conceptualization, data curation, formal analysis, funding acquisition, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Foxcroft LC, Richardson DM, Rejmánek M, Pyšek P. 2010 Alien plant invasions in tropical and sub-tropical savannas: patterns, processes and prospects. *Biol. Invasions* **12**, 3913–3933. (doi:10.1007/s10530-010-9823-7)
2. van Wilgen BW, Zengeya TA, Richardson DM. 2022 A review of the impacts of biological invasions in South Africa. *Biol. Invasions* **24**, 27–50. (doi:10.1007/s10530-021-02623-3)
3. Witt A, Beale T, van Wilgen BW. 2018 An assessment of the distribution and potential ecological impacts of invasive alien plant species in eastern Africa. *Trans. R. Soc. South Afr.* **73**, 217–236. (doi:10.1080/0035919x.2018.1529003)
4. Hejda M, Čuda J, Pyšková K, Foxcroft LC, Nkuna KV, Novoa A, Pyšek P. 2023 Impacts of invasive alien species on riparian plant communities in South African savanna. *J. Trop. Ecol.* **39**, e39. (doi:10.1017/s0266467423000299)
5. Kamaru DN *et al*. 2024 Disruption of an ant–plant mutualism shapes interactions between lions and their primary prey. *Science* **383**, 433–438. (doi:10.1126/science.adg1464)
6. Stutz RS, Croak BM, Proschogo N, Banks PB, McArthur C. 2017 Olfactory and visual plant cues as drivers of selective herbivory. *Oikos* **126**, 259. (doi:10.1111/oik.03422)
7. Stewart PS, Hill RA, Stephens PA, Whittingham MJ, Dawson W. 2021 Impacts of invasive plants on animal behaviour. *Ecol. Lett.* **24**, 891–907. (doi:10.1111/ele.13687)

8. Hale R, Swearer SE. 2016 Ecological traps: current evidence and future directions. *Proc. R. Soc. B* **283**, 20152647. (doi:10.1098/rspb.2015.2647)
9. Adkins SW, McClay A, Bajwa AA. 2019 Biology and ecology. In *Parthenium weed: biology, ecology and management* (eds S Adkins, A Shabbir, K Dhileepan), pp. 7–39. Wallingford, UK: CABI International. (doi:10.1079/9781780645254.0007)
10. Musese LJ, Andrew SM, Shirima DD, Witt A, Kilewa R. 2020 Effects of the abundance of *Parthenium hysterophorus* on the composition and diversity of other herbaceous plant species in Simanjiro Rangeland, Tanzania. *Int. J. Eng. Technol. Manag. Res*. **7**, 11–20. (doi:10.29121/ijetmr.v7.i5.2020.631)
11. Nawaz H *et al*. 2025 Assessing the threat: parthenium adverse effects on biodiversity, human communities, and environmental integrity. *Sch. Bull*. **11**, 21–41. (doi:10.36348/sb.2025.v11i03.001)
12. Reynolds C, Venter N, Cowie BW, Marlin D, Mayonde S, Tocco C, Byrne MJ. 2020 Mapping the socio-ecological impacts of invasive plants in South Africa: are poorer households with high ecosystem service use most at risk? *Ecosyst. Serv*. **42**, 101075. (doi:10.1016/j.ecoser.2020.101075)
13. Timsina B, Shrestha BB, Rokaya MB, Münzbergová Z. 2011 Impact of *Parthenium hysterophorus* L. invasion on plant species composition and soil properties of grassland communities in Nepal. *Flora Morphol. Distrib. Funct. Ecol. Plants* **206**, 233–240. (doi:10.1016/j.flora.2010.09.004)
14. Strathie LW, McConnachie AJ, Retief E. 2011 Initiation of biological control against *Parthenium hysterophorus* L. (Asteraceae) in South Africa. *Afr. Entomol*. **19**, 378–392. (doi:10.4001/003.019.0224)
15. Yimenu S, Gebreyes L, Tana T, Adkins S. 2013 Impact of parthenium weed (*Parthenium hysterophorus* L.) on the above-ground and soil seed bank communities of rangelands in Southeast Ethiopia. *Int. Res. J. Agric. Sci. Soil* **3**, 262–274.
16. Mersie W, Singh M. 1987 Allelopathic effect of parthenium (*Parthenium hysterophorus* L.) extract and residue on some agronomic crops and weeds. *J. Chem. Ecol*. **13**, 1739–1747. (doi:10.1007/BF00980214)
17. Tudor G, Ford AL, Armstrong T, Bromage E. 1982 Taints in meat from sheep grazing *Parthenium hysterophorus*. *Aust. J. Exp. Agric. Anim*. **22**, 43–46. (doi:10.1071/EA9820043)
18. Smit IP, Bond WJ. 2020 Observations on the natural history of a savanna drought. *Afr. J. Range Forage Sci*. **37**, 119–136. (doi:10.2989/10220119.2020.1723695)
19. Tiawoun MAP, Malan PW, Moshobane MC, Ramarumo LJ, Comole AA, Naidoo KK. 2024 Ecological traits and socio-economic impacts of the alien invader weed *Parthenium hysterophorus* L. in South Africa's rangeland ecosystems: a review. *Diversity* **16**, 205. (doi:10.3390/d16040205)
20. Vavra M, Parks CG, Wisdom MJ. 2007 Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *For. Ecol. Manag*. **246**, 66–72. (doi:10.1016/j.foreco.2007.03.051)
21. Coverdale TC *et al*. 2021 Large herbivores suppress liana infestation in an African savanna. *Proc. Natl Acad. Sci. USA* **118**, e2101676118. (doi:10.1073/pnas.2101676118)
22. Cowie BW, Byrne MJ, Witkowski ETF. 2022 Small-scale insights into the above- and below-ground invasion dynamics of *Parthenium hysterophorus* in a South African savanna: the potential role of stocking rate. *South Afr. J. Bot*. **144**, 229–237. (doi:10.1016/j.sajb.2021.08.035)
23. Dhileepan K, Callander J, Shi B, Osunkoya OO. 2018 Biological control of parthenium (*Parthenium hysterophorus*): the Australian experience. *Biocontrol Sci. Technol*. **28**, 970–988. (doi:10.1080/09583157.2018.1525486)
24. Rutherford MC, Mucina L, Powrie LW. 2006 Biomes and bioregions of southern Africa. *Veg. South Afr. Lesotho Swazil.* **19**, 30–51.
25. Steenkamp Y, Wyk B, Victor J, Hoare D, Smith G, Dold T, Cowling R. *Maputaland-Pondoland-Albany*, pp. 219–228. Monterey, CA: Cemex.
26. Ke A, Sibiya MD, Reynolds C, McCleery RA, Monadjem A, Fletcher RJ Jr. 2018 Landscape heterogeneity shapes taxonomic diversity of non-breeding birds across fragmented savanna landscapes. *Biodivers. Conserv*. **27**, 2681–2698. (doi:10.1007/s10531-018-1561-7)
27. McCleery R, Monadjem A, Baiser B, Fletcher R Jr, Vickers K, Kruger L. 2018 Animal diversity declines with broad-scale homogenization of canopy cover in African savannas. *Biol. Conserv*. **226**, 54–62. (doi:10.1016/j.biocon.2018.07.020)
28. Soto-Shoender JR, McCleery RA, Monadjem A, Gwinn DC. 2018 The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. *Biol. Conserv*. **221**, 127–136. (doi:10.1016/j.biocon.2018.02.028)
29. Niedballa J, Sollmann R, Courtiol A, Wilting A. 2016 camtrapR: an R package for efficient camera trap data management. *Methods Ecol. Evol*. **7**, 1457–1462. (doi:10.1111/2041-210x.12600)
30. Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S. 2015 Review: wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol*. **52**, 675–685. (doi:10.1111/1365-2664.12432)
31. Riney T. 1960 A field technique for assessing physical condition of some ungulates. *J. Wildl. Manage*. **24**, 92–94. (doi:10.2307/3797362)
32. Brooks ME, Kristensen K, Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J*. **9**, 378–400. (doi:10.32614/RJ-2017-066)
33. R Core Team. 2024 R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org.
34. Lenth RV, Singmann H, Love J, Buerkner P, Herve M. 2021 Emmeans: estimated marginal means, aka least-squares means. R package version 1.5.1. The Comprehensive R Archive Network. See https://CRAN.R-project.org/package=emmeans (accessed 27 September 2022).
35. Rueden CT, Schindelin J, Hiner MC, DeZonia BE, Walter AE, Arena ET, Eliceiri KW. 2017 ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinform*. **18**, 529. (doi:10.1186/s12859-017-1934-z)
36. Ersts PJ. DotDotGoose, version 1.7.0. American Museum of Natural History, Center for Biodiversity and Conservation. See https://biodiversityinformatics.amnh.
37. Cumming G. 2014 The new statistics: why and how. *Psychol. Sci*. **25**, 7–29. (doi:10.1177/0956797613504966)
38. Ho J, Tumkaya T, Aryal S, Choi H, Claridge-Chang A. 2019 Moving beyond *p* values: data analysis with estimation graphics. *Nat. Methods* **16**, 565–566. (doi:10.1038/s41592-019-0470-3)
39. Barton KE, Koricheva J. 2010 The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. *Am. Nat*. **175**, 481–493. (doi:10.1086/650722)
40. Quintero C, Bowers MD. 2012 Changes in plant chemical defenses and nutritional quality as a function of ontogeny in *Plantago lanceolata* (Plantaginaceae). *Oecologia* **168**, 471–481. (doi:10.1007/s00442-011-2114-x)
41. Boege K, Marquis RJ. 2005 Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends Ecol. Evol*. **20**, 441–448. (doi:10.1016/j.tree.2005.05.001)
42. Ahern JR, Whitney KD. 2013 Sesquiterpene lactone stereochemistry influences herbivore resistance and plant fitness in the field. *Ann. Bot*. **113**, 731–740. (doi:10.1093/aob/mct297)
43. Gershenzon J. 1984 Changes in the levels of plant secondary metabolites under water and nutrient stress. In *Phytochemical adaptations to stress* (eds BN Timmermann, C Steelink, FA Loewus), pp. 273–320. Boston, MA: Springer. (doi:10.1007/978-1-4684-1206-2_10)
44. Gaidet N, Gaillard JM. 2008 Density-dependent body condition and recruitment in a tropical ungulate. *Can. J. Zool*. **86**, 24–32. (doi:10.1139/z07-111)
45. Gaidet N, Lecomte P. 2013 Benefits of migration in a partially-migratory tropical ungulate. *BMC Ecol*. **13**, 36. (doi:10.1186/1472-6785-13-36)
46. Gallivan G, Culverwell J. 1995 Body condition indices of impala (*Aepyceros melampus*): effect of age class, sex, season and. *South Afr. J. Wildl. Res*. **25**, 23–31.

47. Dearing MD, Foley WJ, McLean S. 2005 The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annu. Rev. Ecol. Evol. Syst*. **36**, 169–189. (doi:10.1146/annurev.ecolsys.36.102003.152617)
48. Launchbaugh KL, Provenza FD, Pfister JA. 2001 Herbivore response to anti-quality factors in forages. *J. Range Manag*. **54**, 431–440. (doi:10.2307/4003114)
49. Wells HBM *et al*. 2023 Wild herbivores enhance resistance to invasion by exotic cacti in an African savanna. *J. Ecol*. **111**, 33–44. (doi:10.1111/1365-2745.14010)
50. Parker JD, Burkepile DE, Hay ME. 2006 Opposing effects of native and exotic herbivores on plant invasions. *Science* **311**, 1459–1461. (doi:10.1126/science.1121407)
51. Rossell CR, Patch S, Salmons S. 2007 Effects of deer browsing on native and non-native vegetation in a mixed oak–beech forest on the Atlantic coastal plain. *Northeast. Nat*. **14**, 61–72. (doi:10.1656/1092-6194(2007)14[61:EODBON]2.0.CO;2)
52. Averill KM, Mortensen DA, Smithwick EAH, Post E. 2016 Deer feeding selectivity for invasive plants. *Biol. Invasions* **18**, 1247–1263. (doi:10.1007/s10530-016-1063-z)
53. Glennon K *et al*. 2026 Supplementary material from: Wild ungulate foraging suppresses growth of invasive parthenium weed. Figshare. (doi:10.6084/m9.figshare.c.8304069)