WILDLIFE BIOLOGY

Research article

Impacts of African elephants and other environmental drivers on trees nested in by critically endangered white-backed vultures

Robin M. Cook[1,2], **Edward T. F. Witkowski**[1], **and Michelle D. Henley**[2,3,4]

[1]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa
[2]Elephants Alive, Hoedspruit, South Africa
[3]Applied Behavioural Ecology and Ecosystem Research Unit, School of Environmental Sciences, University of South Africa, Florida, South Africa
[4]Department of Philosophy, Faculty of Humanities, University of Johannesburg, Auckland Park, South Africa

Correspondence: Robin M. Cook (robinmichaelcook@gmail.com)

Wildlife Biology
2025: e01335
doi: 10.1002/wlb3.01335
Subject Editor:
Shyamala Ratnayeke
Editor-in-Chief: Ilse Storch
Accepted 14 November 2024

The decline of white-backed vultures *Gyps africanus* (hereafter termed vultures) across Africa highlights the need to understand their habitat and nesting requirements, especially in protected areas where African elephants *Loxodonta africana* can impact the trees in which vultures build their nests. Our study aimed to assess the impact that elephants have on trees containing vulture nests in the Associated Private Nature Reserves (APNR) of South Africa's savanna system through three separate but interlinked assessments. We first assessed the tree species used by vultures for nesting and compared their size and elephant impact scores between riparian and woodland habitats. We assessed how elephant presence or absence affects the size of *Senegalia nigrescens*, a key tree species, and compared vulture nests in an adjacent elephant-free area. Lastly, we modeled environmental factors influencing vulture nest and tree persistence using data from 2008–2020. Vultures utilised 10 tree species, with riparian trees supporting nests being significantly taller, with larger DBHs, and experienced lower elephant impact compared to woodland trees, which were more heavily impacted by elephants. Less robust species like *S. nigrescens* were more vulnerable to elephant damage, primarily bark-stripping, and less likely to host vulture nests. Our results show that vultures prefer the largest, least impacted trees for nesting, favouring those with greater stability and longevity. We suggest that although elephants influence the overall height range of trees to vultures, strong gusts of wind have a strong negative contribution on vulture nest persistence and that only a relatively small number of trees died during the 12-year study in comparison to fallen nests. We recommend further research into elephant impact thresholds on trees and vulture nest selection. Monitoring treefall and regeneration rates will help predict when vultures may face a shortage of suitable nesting trees.

Keywords: *Gyps africanus*, increasing elephant numbers, *Senegalia nigrescens*, strong winds, tree mortality, vulture nests

NORDIC SOCIETY OIKOS

www.wildlifebiology.org

Introduction

White-backed vultures *Gyps africanus* provide critical ecosystem services to savanna systems as a scavenging species (Ogada et al. 2012, Van den Heever et al. 2021), and are important regional avian biomonitors and an umbrella species for African vultures (Thompson et al. 2021). There have, however, been significant declines in white-backed vulture (hereafter referred to as vultures) numbers, both continentally (Ogada et al. 2016) and regionally within South Africa (Birdlife International 2024). These vultures are now listed as 'Critically Endangered' globally (Birdlife International 2024). Poisoning events have largely contributed to the decline of adult vultures (Ogada et al. 2016, Peters et al. 2023), whilst collisions with powerlines and wind turbines, pylon electrocutions, as well as the acquisition and trade of vulture body parts within traditional medicines, have further exacerbated vulture mortality (Jenkins et al. 2010, Rushworth and Krüger 2014, Mashele et al. 2021).

As a long-lived species, vulture adult survival is essential for population endurance (Monadjem et al. 2013). However, habitat loss, particularly due to human-induced changes to the environment, has placed even greater pressure on protected areas (PAs) to preserve trees suitable for vulture nesting sites (Rushworth et al. 2018). Currently, over 50% of the distribution range of vultures overlaps with PAs in southern Africa (Kane et al. 2022), where, as tree-nesting species, vultures are reliant on locally tall trees, ranging from 7–20 m in height depending on the habitat (Bamford et al. 2009, Johnson and Murn 2023). Tall trees may provide vultures with either social foraging cues (Kendall et al. 2012), or an escape from nest predators (Kemp and Kemp 1975).

White-backed vultures are monogamous, typically nesting in tall trees (Birdlife International 2024). They exhibit loosely colonial breeding behaviour, with pairs nesting within sight of one another (Monadjem and Garcelon 2005). Generally, only one breeding pair occupies a tree, though in some cases, two nests may be found in a single tree (Bamford et al. 2009). Their nests are constructed using sticks and lined with grass. Egg-laying predominantly occurs between April and July, with a clutch usually comprising a single egg, though very rarely two eggs are laid (Murn and Anderson 2008). This species is single-brooded, meaning they produce only one brood per breeding season. Pairs often return to the same nesting site in subsequent years. Breeding success varies significantly, ranging from 43 to 87% (Birdlife International 2024). Given their single-egg clutches and the variability in breeding success, reproductive success may indeed be a limiting factor in the population persistence of white-backed vultures (Monadjem et al. 2013).

In South Africa's savanna system, high densities of nests occur on top of tall trees within the riparian habitat (± 100 m defined buffer zone along major river systems that is influenced by river-related processes; Linstrom 2018), whilst lower densities of nests are found in the woodland habitat varied intermix of grasses and trees (Scholes and Archer 1997) bordering the riparian zone, usually on top of *Senegalia nigrescens* trees (Virani et al. 2010, Vogel et al. 2014, Kendall et al. 2018). Riparian tree species are generally very large in comparison to woodland trees due to increased levels of soil moisture and nutrients (Scholes and Archer 1997). However, concerns exist in South Africa regarding the decline of large trees (> 5 m in height; Shannon et al. 2008) due to African elephant *Loxodonta africana* feeding habits (Asner et al. 2016, Cook et al. 2023) and the implications to vulture populations inside of PAs through tree loss (Monadjem and Garcelon 2005, Rushworth et al. 2018). Understanding nesting distributions and the related elephant impact on these trees helps inform conservation strategies for both white-backed vultures and the broader ecosystem. If vultures show a strong preference for one type of habitat and that habitat is under greater threat from elephants and other environmental factors, conservationists can better prioritise habitat protection and restoration efforts (Swemmer et al. 2023).

Elephants, as ecosystem engineers (Owen-Smith 1988) can alter the structural landscape of savannas through the trimming of tree heights by the removal of branches or by the removal of the large tree component (Guldemond et al. 2017), thereby promoting landscape openness (Gordon et al. 2023). However, in small fenced-off PAs, and/or PAs with high waterhole densities, impact on large trees may be exacerbated due to increased probability of encounters between elephants and large trees (O'Connor et al. 2007). Elephant feeding habits such as bark-stripping and tree toppling can directly kill large trees or leave these trees vulnerable to fire damage and insect infestation, which shorten the lifespan of the tree (Wigley et al. 2019, Das et al. 2022). Recent studies have shown that densities of large trees can decrease in PAs where high densities of elephants exist in a manner where the elephants' impact is not varied on both a spatial and temporal scale (Thornley et al. 2020, Thompson et al. 2022). The reduction of large trees could therefore reduce the availability of suitable nesting trees for vultures and may have negative consequences for the breeding success and sustainability of vulture populations (Kendall et al. 2018, Rushworth et al. 2018, Johnson and Murn 2023).

Very few studies have specifically focused on the impact that elephants have on the trees in which vultures nest, with varying results. Monadjem and Garcelon (2005) found that vultures were not nesting in PAs in Eswatini that contained elephants. However, in Kenya's Masai Mara National Park, Kendall et al. (2018) modelled that suitable tree numbers for vulture nests far outnumbered the number of vulture nesting pairs in the region. Furthermore, in South Africa's Associated Private Nature Reserves (APNR), elephant impact on *S. nigrescens* containing vulture nests did not affect nest persistence over a five-year monitoring period but did drive the long-term decline of the trees' structural integrity to support nests (Vogel et al. 2014).

Given that vultures nest in a variety of tree species in both woodland and riparian habitats (Virani et al. 2010), and that the degree and type of elephant impact varies across tree species (Abraham et al. 2021), it is important to assess the vulnerability of the trees in which vultures nest versus elephant

impact across a multitude of tree species. Furthermore, as previous studies have highlighted the importance of *S. nigrescens* as a commonly-used nesting tree for vultures in southern Africa's savannas (Monadjem and Garcelon 2005, Vogel et al. 2014), additional studies are required to understand the ecological relationships between elephants and vulture nests on *S. nigrescens* trees. No studies to our knowledge have focused on the vulnerability of vulture nests and the tree species in which they nest in comparison to elephant impact, nor examined in-depth how various ecological agents can influence vulture tree and nest persistence over an extended time where elephants occur (12 years for this study).

In addition to elephant impact, other ecological agents may negatively affect tree persistence. The agents include the presence of termites (*Coptotermes* species) (Gould 1993) and shelf-bracket fungus (Hood 2006) within the tree, as well as the presence of ants (*Crematogaster* species), which can also serve as protection agents against herbivory (Palmer and Brody 2013). Previous research has found that elephants tend to impact trees closer to surface water (Van Langevelde et al. 2017) and roads (Khosa et al. 2023), as well as increase their impact on trees during periods of low rainfall (Coetsee et al. 2023).

Therefore, our study aimed to assess elephant impact on trees containing vulture nests in the South African savanna system through three separate but interlinked assessments. Our objectives were to 1) measure the dimensions of nesting trees selected by vultures, as well as the elephant impact scores on these trees, with a comparison of habitat types between riparian and woodland trees (termed: *multispecies assessment*), 2) assess the influence that the presence and absence of elephants have on the morphometrics of *S. nigrescens* trees containing vulture nests, as well as control *S. nigrescens* trees with no vulture nests (termed: *elephant effect*), and 3) investigate the long-term (2008–2020) changes in the number of *S. nigrescens* trees containing vulture nests that co-occur with elephants, in relation to elephant impact and other non-elephant factors influencing their persistence (termed: *persistence trends*).

Material and methods

Study area

The study was conducted in the Associated Private Nature Reserves (APNR) (24°04′–24°55′S; 30°82′–31°48′E) and the neighbouring Air Force Base Hoedspruit (AFB) (24°19′–24°23′S; 31°01′–31°03′E) in the north-eastern region of South Africa (Fig. 1). The APNR (size: 2089 km^2) is a protected area, sharing an open boundary with the Kruger National Park, and includes the private nature reserves of Balule, Klaserie, Thornybush, Timbavati and Umbabat Private Nature Reserves (Fig. 1). The AFB (size:

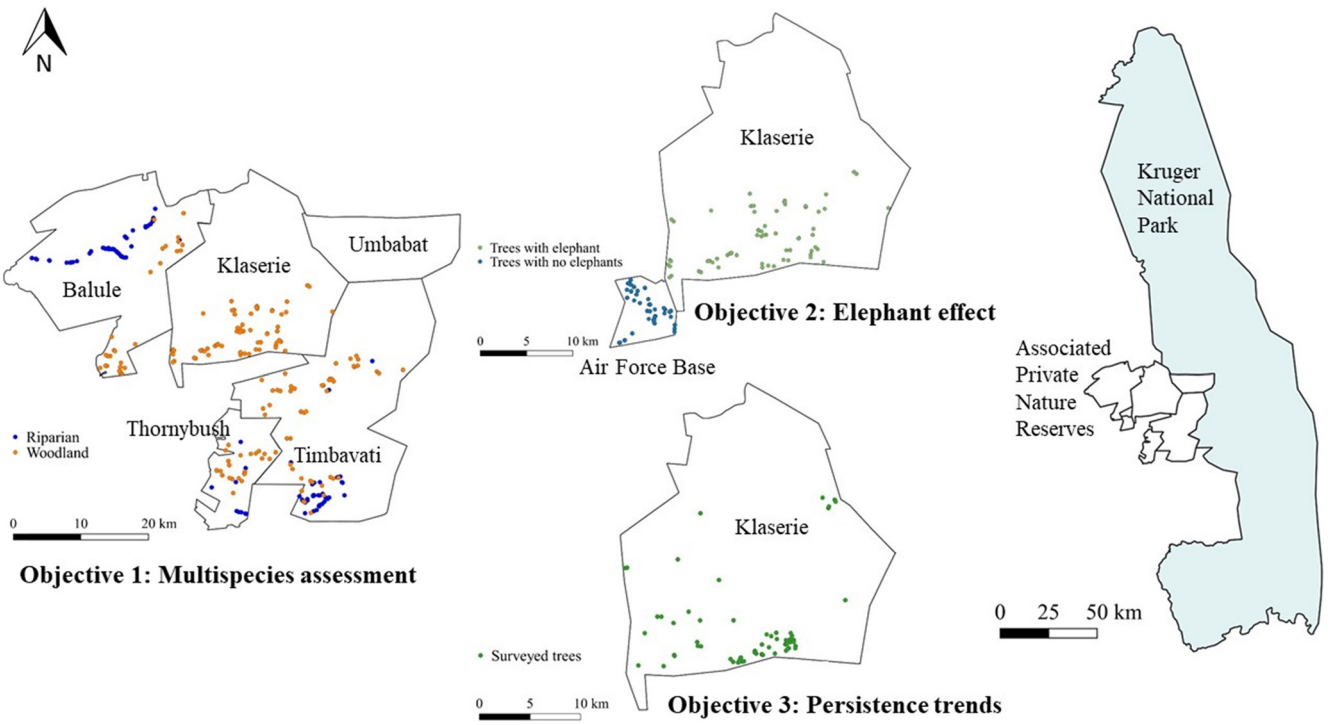

Figure 1. Location of the surveyed trees for each study objective in the Associated Private Natures Reserves (APNR) and Hoedspruit Air Force Base (AFB), bordering South Africa's Kruger National Park. Objective 1 indicates the locations of the surveyed riparian and woodland trees across the APNR. Objective 2 indicates the location of surveyed trees inside of Klaserie Private Nature Reserve (with elephants) and the AFB (without elephants). Objective 3 indicates the location of the original 67 surveyed trees in Klaserie Private Nature Reserve from 2008.

25 km^2) boundary is fenced along the south-western border of the Klaserie Private Nature Reserve (PNR, Fig. 1), and hence has no elephants. The region's mean annual rainfall is 446 mm (range: 176–998 mm), with an average maximum temperature of 28˚C (range: 22–33˚C) (Adeola et al. 2022). Both the APNR and AFB are located within the Granite Lowveld (SVI 3) vegetation unit of South Africa, whilst the APNR also extends into the Phalaborwa-Mopaneveld (SVmp 7) vegetation unit (Mucina and Rutherford 2006). The tallest species of trees within the riparian zone include *Diospyros mespiliformis* and *Schotia brachypetala*, whilst those in the woodland zone include *S. nigrescens* and *Sclerocarya birrea* (Mucina and Rutherford 2006). The APNR and AFB fall within the Olifants River catchment, whilst the APNR is dissected by prominent non-perennial tributaries such as the Klaserie and Timbavati rivers (Marr et al. 2017). Many artificial waterholes exist in the APNR, meaning that water here is permanently available to elephants (Parker and Witkowski 1999, Henley 2014).

There are an estimated 220 active vulture nests in the APNR (extracted from the APNR Annual Census Reports), with an additional 40–50 breeding pairs in AFB (Thompson unpubl.). The term 'active' refers to the nest having been occupied by vultures for breeding purposes between survey years.

The APNR's elephant population ranges between 3000 and 3500 individuals (unpublished 2021 census data provided by the APNR), forming part of a metapopulation of over 40 000 individuals in the Great Limpopo Transfrontier Conservation Area (GLTFCA) (GLTFCA 2022). Elephant numbers in the APNR are significantly higher than the surrounding adjoining protected areas of the GLTFCA due to the high density of artificial waterpoints which discourages elephants from dispersing from the APNR.

The locations of all surveyed trees in the APNR were obtained and ground-truthed from the previous years' aerial surveys conducted by APNR management, as well as through the historical database of the NGO *Elephants Alive*. The entire APNR falls under an overarching general elephant management plan (GLTFCA 2022).

Objective 1 (*multispecies assessment*) was addressed across the entire APNR where a greater diversity of trees used by vultures occurred than within any one reserve forming part of the collective whole. Riparian trees for this objective were predominantly located along the Olifants and Timbavati Rivers' riparian zones (Fig. 1). No known vulture trees were present in Umbabat PNR during the time of these surveys, which is a predominantly Mopaneveld-dominated PNR with a lack of suitable nesting tree species for vulture colonies (Mucina and Rutherford 2006).

Objective 2 (*elephant effect*) was addressed inside the Klaserie PNR and the AFB where comparisons in the presence and absence of elephants could be made for the longest period (Fig. 1). Both the Klaserie PNR and AFB surveyed trees are located within the woodland zone only, ensuring a direct comparison of environmental components on the presence and absence of elephants. *Senegalia nigrescens* was selected as the tree species in question as it is 1) the most abundant tree species containing vulture nests within the APNR, and 2) is the prime tree species utilised by vultures for nesting purposes within the Klaserie PNR and AFB, respectively.

Objective 3 (*persistence trends*) was addressed inside the Klaserie PNR as this was the original site for annual vulture tree monitoring in the APNR by the NGO *Elephants Alive* starting 2008 (Fig. 1). The location of these trees was reflective of those recorded during the 2008 Klaserie PNR aerial census.

Field methods

Objective 1: multispecies assessment

Surveys were conducted across the APNR to investigate both the morphometric traits and elephant impact scores on trees of different species utilised by vultures for nesting purposes (Fig. 1). Individuals of all tree species that had contained active vulture nests in either 2019 or 2020 (n = 266) were assessed across the Balule, Klaserie, Thornybush, and Timbavati PNRs in late October and early November of the respective years to minimise any disturbance to vultures breeding on the nest.

At each tree the following methodology was conducted: tree location was marked using a global positioning system (GPS) and tree species was identified; the tree's stem diameter at breast height (DBH, 1.3 m) (cm) was measured, whilst tree height (m) was measured using the *VolCalc* software (Barrett and Brown 2012). For large riparian trees with multi-stem diameters (example: *Ficus sycomorus* subsp. *sycomorus*), the diameter of the stem containing the nest was measured. Elephant impact on each tree was measured using published impact scoring practices (Table 1, Walker 1976 (adapted); Helm and Witkowski 2013).

Objective 2: elephant effect

Surveys were conducted in the Klaserie PNR and the AFB to investigate the impact that elephants have on *S. nigrescens* trees, both with and without vulture nests (Fig. 1). In late

Table 1. Scoring system for elephant impact on large trees (Walker 1976 (adapted); Helm and Witkowski 2013).

Score	Score description
0	No impact
1	< 50% of the bark around the main stem's circumference has been removed and/or secondary branches have been broken off
2	> 50% of the bark around the main stem's circumference has been removed, or one primary branch has been broken off
3	> 50% of the bark around the main stem's circumference has been removed and one primary branch has been broken off, or more than one primary branch has been broken off
4	The tree has had its main stem snapped but is coppicing or alive
5	Tree is dead

October and early November 2020, we surveyed all known *S. nigrescens* in Klaserie PNR that had contained an active vulture nest (recent signs of faeces under the nest or broken eggshells) in either the 2019 or 2020 surveys (n = 63). Each tree had its morphometric measurements recorded (described in objective 1), and elephant impact scores were recorded (Table 1). These trees were termed 'Vulture trees (with elephants)'. We conducted the same assessments on the closest 1–4 *S. nigrescens* individuals within a radius of 100 m from the vulture nest tree (average = 2.2 control trees per vulture tree), where one tree per cardinal direction point from the nest was measured where possible. We selected trees ≥ 4 m in height as the lower limit for surveyed trees to eliminate saplings from the study (Watson et al. 2020). A total of 148 of these trees were recorded and were termed 'Control trees (with elephants)'.

In November and December 2022, permission was granted by the AFB to conduct morphometric assessments on all the known vulture nests within the base (locations provided by AFB). Due to the strict policies surrounding entry into the AFB and Covid-19 restrictions, only a single season of survey could be completed, placing limitations on examining additional factors on tree and vulture nest persistence overtime. Forty *S. nigrescens* with vulture nest trees were located and had their heights and DBHs measured (Fig. 1) and were termed 'Vulture trees (no elephants)'. Using the same approach for surveying control trees in Klaserie PNR, we measured the height and DBH of 120 surrounding *S. nigrescens*, termed 'Control trees (no elephants)'.

Objective 3: persistence trends

To investigate how environmental co-variates have affected the persistence trends of vulture nests and the trees containing them, we selected all *S. nigrescens* trees that contained vulture nests in the Klaserie PNR in 2008 according to the annual census records (n = 67) and conducted annual surveys on these trees and nests from 2008–2020 (Fig. 1). Each tree had a single vulture nest in 2008. The historical data collected from these surveys took place between August and September each year. Given our concerns over the seasonal period of this historical data collection, when the adults vultures may be present on the nest, we subsequently adjusted our surveys to October–December (Objectives 1 and 2) from 2020 onwards to avoid disturbing the adult vultures on the nests. With this adjusted observation period, we applied for and were granted an ethical waiver from the University of the Witwatersrand, Johannesburg Animal Ethics Committee (waiver-18-01-2021-O).

The following information was recorded in the historical data set: tree height (m), DBH (cm), and elephant impact score, which was the previous year's impact score (Table 1). The following additional covariates were also included: presence of ants (*Crematogaster* species), as this species may weaken trees and prevent stripped bark from healing following elephant impact (Wigley et al. 2019); termites (*Coptotermes* species), whose presence in a tree compromises the tree's structural integrity by tunnelling through the wood, causing internal decay and weakening the tree's overall stability (N'Dri et al. 2011); and shelf-backet fungus, which siphons essential nutrients from a tree while decaying its internal wood, severely weakening the tree's structural integrity and making it more susceptible to breakage or collapse (Seymour and Joseph 2019). Lastly fire scar presence was recorded on the tree trunk, as fire can compromise a tree's main stem by damaging its bark and inner tissues, leaving it weakened and more vulnerable to elephant impact or desiccation (Das et al. 2022).

We approached all trees carefully, minimising noise and disturbances and leaving as soon as the necessary data was collected. We then used the 'Nearest Euclidean distance to feature' in ArcGIS to record each tree's distance to the nearest surface water, and to the nearest road. Trees located closer to water sources have a higher probability of receiving elephant impact in comparison to trees located further away (O'Connor et al. 2007). Elephant bulls, who are more likely to impact large trees make use of roads and thus trees located closer to roads have a higher probability of being impacted by elephants versus trees located further away (Coetzee et al. 1979). Historical rainfall data was obtained from the Klaserie PNR warden. Lastly, after the surveys revealed a trend of nests falling after major windstorms, we recorded the maximum gust speed (km h^{-1}) for the study site each year, as well as the number of days that gust-winds (> 72 km h^{-1}; Mitchell 2013) occurred annually (South African Weather Service, unpubl.).

Data analyses

Statistical analyses were performed in R version 4.3.0 (www.r-project.org) and were considered significant at $p < 0.05$. For the *multispecies assessment*: trees were grouped into 'Riparian' and 'Woodland' habitat categories, based on the vegetation zones into which they were recorded (Bamford et al. 2009, Table 2). The height, DBH and elephant impact score measurements were then pooled within the Riparian and Woodland groupings. Mann-Whitney U-tests (Shapiro–Wilk test; $p < 0.05$) were then used to test for significant differences between the height, DBH, and elephant impact scores between Riparian and Woodland trees.

For the *elephant effect*, we performed Kruskal–Wallis one-way analysis of variance tests, with Dunn's multiple comparison post-hoc test, to compare the differences in tree height and DBH of the four categories of both the control and vulture *S. nigrescens* trees that were surveyed with and without the presence of elephants. To calculate the variability of tree heights and DBH sizes used by vultures with and without the presence of elephants, we calculated the coefficient of variation of each of these four forementioned categories. A Mann–Whitney U-test was used to compare elephant impact scores between the Vulture trees (with elephants) and the Control trees (with elephants), as well as between the Vulture and Control trees with elephants versus those without elephants.

For the *persistence trends*: A Kaplan–Meier survival analysis ('survival' package, Therneau 2024) was used to test for

Table 2. Tree species utilised as nesting trees by white-backed vultures *Gyps africanus* in the Associated Private Nature Reserves (APNR), South Africa, during the 2019 and 2020 surveys. Tree height, diameter at breast height, and elephant impact scores (mean ± SD) are presented for each tree species.

Tree species	Number of trees with nests	Tree height	Stem diameter at breast height	Elephant impact score (range: 0-5)	Habitat category
Diospyros mespiliformis	38	15.9 ± 3.1 m	101.1 ± 35.8 cm	0.2 ± 0.6	Riparian
Faidherbia albida	3	16.2 ± 1.5 m	81.7 ± 4.8 cm	1	
Ficus sycomorus subsp. *sycomorus*	24	17.3 ± 2.8 m	121.4 ± 35.9 cm	1.4 ± 0.7	
Philenoptera violacea	7	12.1 ± 1.8 m	64.6 ± 12.6 cm	0	
Phyllogeiton discolour	4	16.9 ± 2.2 m	93.4 ± 24 cm	1 ± 0.8	
Xanthocercis zambesiaca	2	18.9 ± 3.8 m	117 ± 3.1 cm	2 ± 1.4	
Riparian total	102				
Balanites maughamii	6	11.7 ± 1.9 m	61 ± 14.5 cm	0.8 ± 0.4	Woodland
Combretum imberbe	2	11.8 ± 1.3 m	62 ± 21.2 cm	0	
Sclerocarya birrea subsp. *caffra*	8	12.8 ± 1.7 m	77.9 ± 18.1 cm	0.4 ± 0.7	
Senegalia nigrescens	148	11.9 ± 1.5 m	60.3 ± 13.1 cm	1.9 ± 1.4	
Woodland total	164				

significant differences between the persistence proportions of vulture nests and the *S. nigrescens* trees they were found on from 2008–2020. The death of a tree and/or collapse of a nest was considered truncated (1), whilst tree and nest persistence were considered censored (0) for our analyses. Where significant differences occurred, the Holm–Sidak post-hoc method was applied (Holm 1979). Annual mortality rates of trees and nests were calculated as: $\text{mortality} = 1-(1-\text{mortality}_i)^{1/\text{years}}$, where mortality_i refers to the overall mortality during the specified period of study, and years referred to the number of years since the study had commenced (Swemmer et al. 2023).

We then performed Cox proportional-hazard models (Cox model, 'coxme' R package, Therneau 2023) independently on the trees and the nests to analyse how various covariates have affected their persistence between 2008 and 2020. These multivariable models enable a group of co-variates to be used to measure time-to-event outcomes (Fisher and Lin 1999), and include 1) a hazard (risk) function, 2) a time component, and 3) an event component (Kleinbaum and Klein 2012). The death of a tree or collapse of a nest were considered truncated (1) events, whilst nest and tree persistence were considered censored (0). Both tree height and DBH were used as co-variates in the Cox models due to the low correlation score between them (Pearson's correlation: r = 0.51). In addition, the following co-variates were used for both the tree and nest Cox models: distance to road (continuous), distance to water (continuous), fire scar presence (categorical), termite presence (categorical), shelf-bracket fungi presence (categorical), ant presence (categorical), previous elephant impact score (categorical), mean annual rainfall (continuous), and maximum wind gust speed (continuous). All continuous co-variates were scaled and centred prior to modelling to ensure comparability across variables and to improve model convergence. This was achieved by subtracting the mean from each value and dividing by the standard deviation.

Stepwise backward selection was used to obtain the models' final versions, where we systematically eliminated the highest p-value from the model before repeating the modelling procedure. Final models were then confirmed through a forward selection process, which involved obtaining p-values through likelihood ratio tests of the full model with the selected co-variate versus the model without that co-variate, giving consistent regression parameter estimates (West et al. 2007).

Welch's t-tests were used to compare differences between the DBHs of living and dead trees, as well as differences of tree heights between trees with persisting nests and trees with fallen nests.

Results

Multispecies assessment

We recorded 266 vulture nests across 10 tree species in the APNR in 2019 and 2020 (Table 2). *Senegalia nigrescens* was the most prolific species (n = 148; 55.6%), followed by *D. mespiliformis* (n = 38; 14.3%). Six of the ten tree species were classified as Riparian trees (n = 102; 38.3%), whilst four species were Woodland trees (n = 164; 61.7%) (Table 2).

Trees containing vulture nests had a height range of 7.4–22.8 m, with Riparian trees significantly taller (mean ± SD: 15.25 ± 3.4 m) than Woodland trees (11.96 ± 1.53 m) ($U = 2829.5$, $p < 0.001$, Fig. 2a). DBH sizes ranged from 32–204 cm, with the mean DBH of the Riparian trees (98.3 ± 34.6 cm) significantly wider than those of the Woodland trees (61.2 ± 13.9 cm) ($U = 2172$, $p < 0.001$, Fig. 2b).

No elephant impact was found on 75 of the 266 surveyed trees (28.2%), including all the *Philenoptera violacea* and *Combretum imberbe* trees. Of the 191 trees (71.8%) with elephant impact, bark-stripping was the most common impact type (80.9%), followed by primary branch breakage (17.7%) and uprooting (1.4%). Of the bark-stripped trees, 55.6% had a bark-stripping score of > 50%, and one individual tree (*S. nigrescens*) had died from bark-stripping. Elephant impact scores were significantly higher on the Woodland trees in

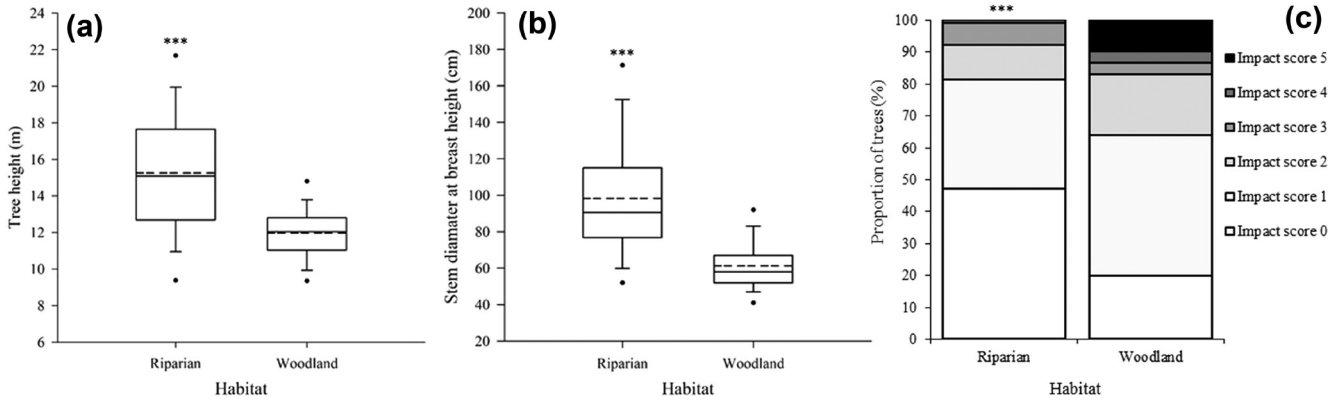

Figure 2. Comparison of (a) tree height, (b) stem diameter at breast height, and (c) elephant impact scores of Riparian (n = 102) and Woodland (n = 164) trees containing white-backed vultures *Gyps africanus* nests in the Associated Private Nature Reserves (APNR), South Africa. Box plots are presented with the median (solid) and mean (dashed lines) values, as well as the 5th and 95th percentiles (black dots). *** $p < 0.001$.

comparison to the Riparian trees ($U = 4861$, $p < 0.001$, Fig. 2c). The highest impact scores were recorded on *S. nigrescens,* and lowest impact scores recorded on *C. imberbe* and *P. violacea* (Table 2). There were no Riparian trees with the most severe impact score of 5, unlike Woodland trees with 9.6%.

Elephant effect

A total of 63 *S. nigrescens* trees containing vulture nests and 148 trees unoccupied by vultures were surveyed in the Klaserie PNR, where elephants were present. In contrast, 40 *S. nigrescens* trees containing vulture nests, and 120 unoccupied trees were assessed in the AFB, where elephants were absent. *S. nigrescens* trees selected for by vultures for nesting purposes were significantly larger in height (Dunn's multiple comparison test: $p < 0.001$) and DBH (Dunn's multiple comparison test: $p < 0.001$) versus the control trees in both Klaserie PNR and AFB (Fig. 3a, b). In Klaserie PNR, the mean height of the vulture trees was 12 ± 1.9 m, whilst the control trees' mean height was 11 ± 1.4 m (Fig. 3a). In AFB, the mean height of the vulture trees was 12.2 ± 1.9 m in comparison to the control trees of 10.9 ± 1.9 m (Fig. 3a). The heights of the vulture trees in Klaserie PNR and AFB were not statistically different ($p = 0.96$, Fig. 3a), however the coefficient of variation was lower for the trees with elephants (11.7%) versus trees without elephants (15.6%). A similar trend was observed for the control trees, where the trees with elephants had a smaller coefficient of variation (13.0%) in comparison to trees without elephants (17.1%).

Vultures selected trees of similar DBH sizes ($p = 0.94$) in both Klaserie PNR (58.6 ± 6 cm) and AFB (57.6 ± 10.8 cm, Fig. 3b). The coefficients of variation for DBH were similar for the vulture trees in Klaserie PNR (18.8%) and AFB (20%).

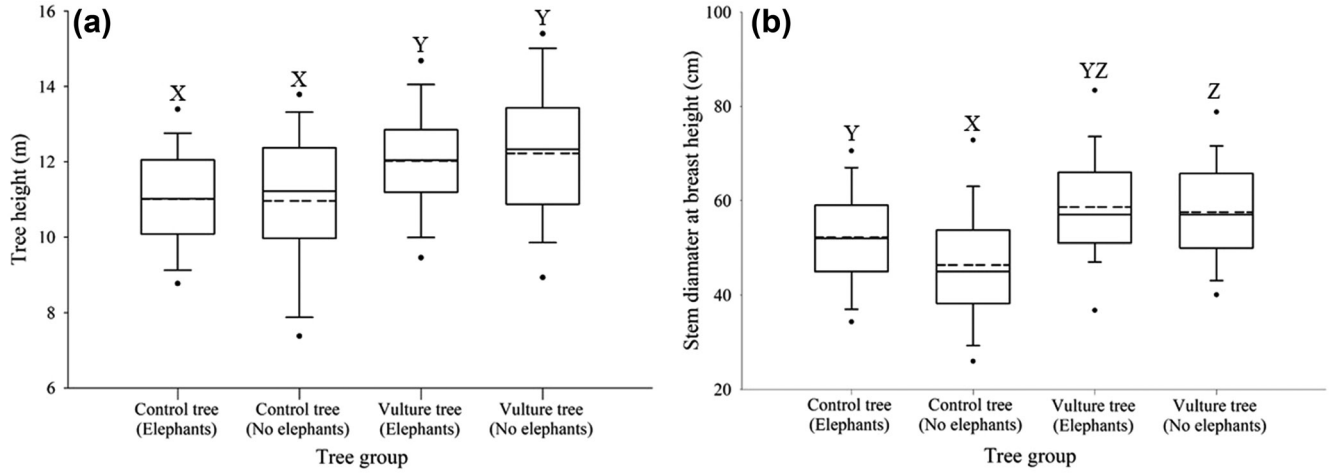

Figure 3. Comparison of *Senegalia nigrescens* (a) height and (b) stem diameter at breast height measurements for trees with and without white-backed vulture *Gyps africanus* nests in Klaserie Private Nature Reserve (with elephants) and the neighbouring Air Force Base (AFB) Hoedspruit (no elephants), South Africa. Box plots are presented with the median (solid) and mean (dashed lines) values, as well as the 5th and 95th percentiles (black dots). Different letters indicate significant differences at $p < 0.05$.

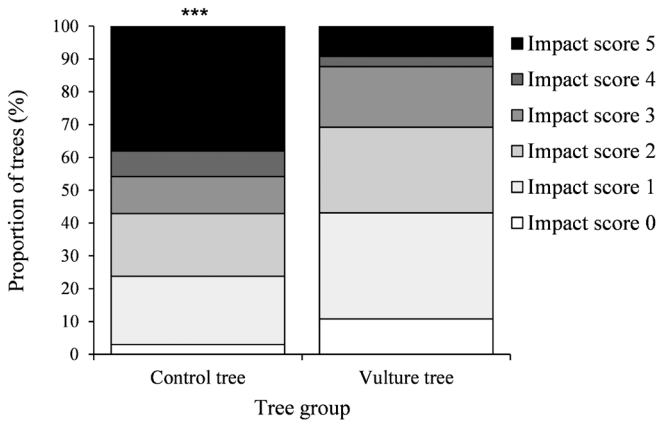

Figure 4. Comparison of elephant impact scores on *Senegalia nigrescens* trees with and without white-backed vulture *Gyps africanus* nests in Klaserie Private Nature Reserve, South Africa. *** $p < 0.001$.

Vulture nests occurred on trees with significantly less elephant impact in comparison to control trees in Klaserie PNR ($U = 3431$, $p < 0.001$, Fig. 4). Of the vulture trees, 10.8% had not been impacted by elephants, whilst 12.3% had elephant impact scores of 4 or 5, signifying high levels of impact. Comparatively, every control tree had some form of elephant impact, whilst a large proportion (45.8%) of them had elephant impact scores of 4 or 5.

Persistence trends

Between 2008 and 2020, the number of days with gust-winds in the Klaserie Private Nature Reserve ranged from 0 to 4 days per year, with the maximum of 4 days occurring in 2010, 2011, 2014, and 2019. In contrast 2009 and 2012 recorded no days with gust-winds (Table 3).

Nest persistence was significantly lower in comparison to tree persistence (Log-rank test = 52.13, d.f. = 1, $p < 0.001$, Fig. 5). After 12 years, 51 of the 67 *S. nigrescens* trees (73.1%) that had originally held active vulture nests were still alive, whilst 16 trees died due to elephant impact (Fig. 5). Only 10 of the original 67 vulture nests (13.9%) were still in existence after 12 years (Fig. 5). Mean nest persistence was 4.1 ± 2.2 years, whilst 15.9% of the 57 dilapidated nests were rebuilt by vultures, at a median time of two years after the collapse of the nest. Nest persistence declined annually at 15.2% in comparison to the trees at 2.5%. Substantial nest declines occurred within the 2010–2011 and 2012–2014 surveys, whilst tree numbers declined at a steady, albeit slower rate than nests between the 2010–2014 surveys (Fig 5). Of the dead trees, 78.6% died from bark-stripping, whilst uprooting constituted 14.3% of the deaths and main stem snapping 7.1%. For the period of 2016–2019, no vulture tree within this survey died (Fig. 5).

According to the reduced tree persistence Cox model, DBH and maximum gust speed were the only co-variates which significantly influenced tree persistence, where an increase in DBH resulted in greater tree persistence, whilst increased wind gust speeds decreased tree persistence across the 12-year period (Table 4). The mean DBH of the dead trees (measured where bark was still attached) during this study was 48.7 ± 11 cm, which was significantly smaller than the mean DBH of the surviving trees (62.3 ± 11 cm) ($t = 4.5$, $p < 0.001$).

Nest persistence, according to the reduced Cox model, improved with an increase in tree height (Table 4), where mean tree height of the fallen nests (12.4 ± 1.6 m) was significantly smaller than trees with persisting nests (14.1 ± 1 m) ($t = 4.4$, $p < 0.001$). Nests were, however, vulnerable to high gusts of wind (Table 4). Maximum wind gust speed ranged from 65.6–101.5 km h^{-1} across the study period, with the median maximum gust wind speed for fallen nests at 72 km h^{-1}. Between 2011 and 2015, the average maximum gust speed of 80.4 km h^{-1} was notably higher than the median maximum gust speed responsible for causing nest falls, contributing to the significant nest declines observed during this period. Interaction terms between tree height and maximum gust speed were included in the model to assess potential synergistic effects. However, these terms did not produce statistically significant results ($p = 0.82$) and were subsequently removed from the final model for parsimony. Previous elephant impact scores on the trees did not significantly affect vulture nest persistence. We re-ran the Cox models for the periods 2010–2011 and 2012–2014, during which major nest falls occurred, and found that, consistent with the main model, tree height (2010–2011: $p = 0.02$; 2012–2014: $p < 0.0001$) and wind gust speed (2010–2011: $p = 0.001$; 2012–2014: $p = 0.02$) were the two significant covariates associated with nest fall.

Discussion

Elephants' selective foraging nature on large trees, both on a structural- and species- related basis, signifies a potential threat to the persistence of trees selected by vultures if such trees are not being replaced through regeneration over time, although this threat may differ depending on the selected size and species of tree by the vultures (Shannon et al. 2008). As vultures face numerous continental and regional threats (Ogada et al. 2016), understanding how elephants impact vulture nesting trees is important for the conservation and management of this critically endangered species (Rushworth et al. 2018).

Overall, we found that vultures made use of a wide range of tree heights (7.4–22.8 m) and DBHs (32–204 cm), suggesting a degree of flexibility in tree size preferences. Particularly,

Table 3. Number of gust-wind days in Klaserie Private Nature Reserve, South Africa, between 2008–2020.

Year	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Days	2	0	4	4	0	3	4	2	3	3	1	4	3

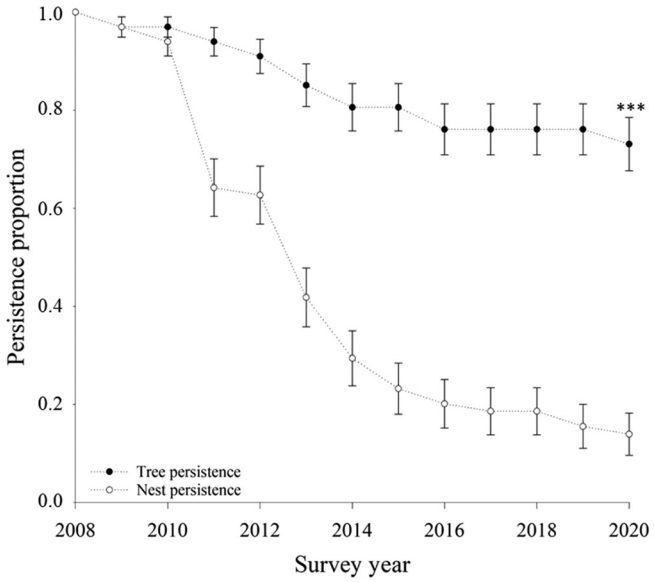

Figure 5. Comparison of the persistence proportions of *Senegalia nigrescens* and white-backed vulture (*Gyps africanus*) nests between 2008 and 2020 in Klaserie Private Nature Reserve, South Africa. *** $p < 0.001$.

riparian trees containing vulture nests had significantly taller heights, larger DBHs, and lower elephant impact scores in comparison to woodland trees with vulture nests. During the dry season, both riparian- and woodland- tree' saplings can be subjected to intense herbivory pressures by browsers and mixed feeders such as impala *Aepyceros melampus*, causing 'bottleneck' effects in the size class demographics (Moe et al. 2009, Turner et al. 2022). Giraffe *Giraffa camelopardalis*, impala and other meso-herbivores are known to browse heavily on accessible foliage of smaller woody plants (Witkowski 1983, Miller 1995). Excessive elephant impact to smaller adult riparian trees may further enhance this 'bottleneck' effect (Teren et al. 2018), and amplify the importance of the largest trees for vulture nesting sites. As shorter trees could put vulture eggs and chicks at risk to predation by terrestrial predators such as leopards *Panthera pardus* and chacma baboons *Papio ursinus* (Wolter and Howard 2019) and be subjected to increased mega- and meso-herbivore impact, an understanding of the morphological differences between riparian versus woodland trees is required when considering the implications of nest site selection by and availability to vultures.

Senegalia nigrescens are often the tallest trees in the woodland habitat and have been recorded as the preferred tree species for vulture nests in various woodlands in South Africa (Kemp and Kemp 1975, Vogel et al. 2014, Rushworth et al. 2018). Our findings concur that in woodland areas, *S. nigrescens* was the most abundant tree species selected by vultures as nesting sites. Within the APNR, Greyling (2004) showed that although elephant bulls remove more plant parts when feeding on this species, family units had a higher overall impact score. *Senegalia nigrescens* had a medium acceptance index to both bulls and family units of elephants when compared to other woodland species. As *S. nigrescens* is a relatively smaller, less robust tree species compared to riparian trees, though not particularly small for savanna woodlands, it is frequently bark-stripped and less frequently felled by elephants (Das et al. 2022). Elephants can potentially have an adverse effect on the availability of large mature *S. nigrescens* within the APNR (Cook et al. 2023). Individual trees that are < 11 m in height are particularly vulnerable to being pushed over by elephants (Shannon et al. 2008). However, our results suggest that, given the significant difference in the persistence rate of vulture trees versus vulture nests, elephant impact is not yet directly affecting the breeding potential of vultures but could be having an indirect influence on vulture nesting behaviour as vultures appear to select the largest trees with the lowest elephant impact scores.

Over time, excessive impact on large trees by megaherbivores, concurrently with reduced recruitment into older age classes of selected woody species, could lead to a reduction in suitable nesting sites for white-backed vultures (Monadjem and Garcelon 2005, Kendall et al. 2018, Seloana et al. 2018) and other tree-nesting birds like lappet-faced vultures *Torgos tracheliotos* (Rushworth et al. 2018) and martial eagles *Polemaetus bellicosus* (Eeden et al. 2017). In protected areas with high elephant densities, abundant waterholes and fence edge effects, elephants' impact on the structural diversity of large trees, combined with increased numbers of water-dependent mixed feeders like impala affecting woody plant recruitment (Archibald et al. 2021), could exacerbate the need for suitable nesting sites for vultures. Although a healthy rate of recruitment for *S. nigrescens* has previously been recorded in Klaserie PNR (Vogel et al. 2014), no recent studies have been conducted on recruitment rates. Other environmental factors such as fires can also keep smaller trees in the fire trap zone of 1–3 m (Levick and Asner 2013), thereby preventing older and taller trees from being replaced in the system over time (Helm et al. 2011b). Future research is needed to not only understand the lack of recruitment due to seedling predation over time (Greyling 2004, Helm et al. 2011a), but how browsing apart from elephants and 'fire traps' (Midgley et al. 2010) are preventing the regeneration of tall trees when comparing woodland to riparian areas, all of which influence the nesting sites of vultures over time. Comprehensive tree height demographics for important vulture nesting tree species at a landscape scale are required to understand where missing size classes are occurring and whether these missing size classes are being created by external agents such as drought (Coetsee et al. 2023), seed predation by rodents (Helm et al. 2011a), seedling herbivory by meso-herbivores (Archibald et al. 2021), intense fires (Jacobs and Biggs 2001), or elephant herbivory (Shannon et al. 2008). If woodland tree recruitment continues to decline, irrespective of the environmental drivers, vultures may be forced to rely more heavily on riparian areas for nesting. Studies are also needed to understand whether vultures can compensate for a loss of suitable nesting sites by accessing suitable trees outside of protected areas. To better understand the potential long-term

Table 4. The reduced Cox proportional-hazards models (with coefficients, hazard ratios, standard errors, and z- and p-values) with the significant co-variates and previous elephant impact affecting the persistence of *Senegalia nigrescens* trees and white-backed vulture *Gyps africanus* nests between 2008 and 2020 in Klaserie Private Nature Reserve, South Africa.

Variable	Coefficient	Exp (coefficient/ hazard ratio)	Standard error	z-value	p-value
Tree persistence					
Diameter at breast height (DBH) (cm)	−0.09	0.92	0.03	−3.37	$p < 0.001$
Maximum wind gust speed (km h^{-1})	0.09	1.09	0.03	3	$p < 0.01$
Previous elephant impact	0.26	1.3	0.3	0.9	0.37
Nest persistence					
Tree height (m)	−0.35	0.7	0.09	−3.72	$p < 0.001$
Maximum wind gust speed (km h^{-1})	0.03	1.03	0.02	2	$p < 0.05$
Previous elephant impact	−0.07	0.93	0.13	−0.56	0.57

impact of these trends, we recommend developing a predictive model that incorporates elephant impacts, tree recruitment rates, and vulture nesting preferences to assess future availability of nesting trees and its implications for vulture conservation.

When comparing protected areas with- (Klaserie PNR) and without (AFB) elephants, we found there was less variation in tree heights selected by vultures in the protected area with elephants. This indicates that elephants could be having a 'trimming' effect on the tree height classes available to vultures, indicative of the lower CV values of tree heights with elephants versus trees without elephants. The lower CV levels for trees containing vulture nests, both with and without elephants, in comparison to their control counterparts, also indicates that vultures are highly selective of various morphological characteristics of trees such as tree height and stem diameter size, even when the structural diversity of trees is being lowered by elephants. It is also worth noting the relatively high density of trees containing vulture nests in the small area of the AFB versus that of the APNR. This is likely due to several factors occurring within the APNR to limit tree densities, including elephant herbivory and previous intense fires within the APNR (Cook et al. 2023), as well as increased herbivory pressure on seedlings by browsers (Helm and Witkowski 2012). Whilst beyond the scope of this study, recent research in the APNR has shown that elephant-induced tree loss increases in drier regions, which experience less mean annual rainfall in comparison to wetter regions (Cook et al. 2023). Elephant impact on more vulnerable trees such as *S. nigrescens* containing vulture nests may be more prevalent in these drier regions.

Our results suggest that strong gusts of wind may be a primary cause of vulture nest collapse in the APNR, and a contributor to tree collapse. Previous research on raptors in the Mediterranean (Martínez et al. 2013) and vultures in West Africa (Daboné et al. 2019) have illustrated how strong winds can be a major cause of continued nest collapse, and personal observations in the APNR have revealed that > 20% of surveyed vulture nests can collapse in a single year after storms, usually collapsing along with the supporting secondary branches (Cook et al. unpubl.). Whilst rebuilding or abandoning nests is not uncommon among vultures (Chomba and M'Simuko 2013), the projected increase of wind speeds in the north eastern regions of South Africa because of climate change may be a potential concern for future vulture breeding success (Herbst and Rautenbach 2015). It is noted though that the use of camera traps in future studies will provide more clarity on this matter, as other agents such as chacma baboons may also be responsible for nest collapse (Wolter and Howard 2019). Whilst strong wind gusts may be an annual rare event (South African Weather Service, unpubl.), they do have capability to dislodge vulture nests from their trees (Cook et al. unpubl.). This, however, may not kill the adult vultures, and so the population would be expected to remain viable (Bamford et al. 2009).

Major windstorms have also been responsible for up to 11% of tree mortality in research sites in the Kruger National Park (Turner et al. 2022). The probability of wind-induced tree mortality, however, can be increased by elephant impact such as bark-stripping, as this weakens the tree's robustness (Hofmeyr 2003). Lastly, the annual mortality of the 67 surveyed *S. nigrescens* containing vulture nests between 2008–2020 (2.5% per annum) was relatively smaller in comparison to recent research by Cook et al. (2023) on the annual mortality rate of 833 *S. nigrescens* across the APNR during the same period (4.9% per annum). The relatively large size of the trees selected for by vultures for nesting purposes in comparison to the surrounding trees may result in these trees being less likely to being toppled or snapped by an elephant, with bark-stripping and its secondary consequences (tree desiccation, insect invasion, fire damage) being the more likely contributor to eventual tree death.

Management implications

Due to the numerous waterholes available to elephants and meso-herbivores in the APNR (Parker and Witkowski 1999), there is concern that elephant impact on the environment is becoming homogenised (Linden et al. 2023) while concurrently seedling predation by water dependent herbivore species could be exacerbated in water saturated environments (Archibald et al. 2021). The impact of elephants on the large individual trees nested in by vultures appears to be species specific, with the relatively shorter woodland tree species more at risk to elephant impact versus the taller riparian species. However, recent trends do indicate a general decline

in overall large tree (≥ 5 m) availability due to a combination of elephant- and fire- impact, as well as potential water stress from the most recent drought (Cook et al. 2023). Furthermore, whilst distance to roads did not feature as significant in our model, the high road density in the APNR likely leads to a uniform effect of elephant impact, as elephants frequently use roads (Coetzee et al. 1979).

Although the previous year's elephant impact score did not emerge as a significant co-variate influencing tree and nest persistence, this may be because vultures in the APNR typically nest in large *S. nigrescens* trees, which are generally taller than the more vulnerable 5–8 m height class that is more susceptible to elephant impact (Vogel et al. 2014, Turner et al. 2022). Bark-stripping is the most common elephant impact type observed on trees used by vultures for nesting. Whilst bark-stripping poses a threat to these larger trees through insect and fungal infestations (Wigley et al. 2019) and desiccation from fire (Helm et al. 2011b), the slow process of bark-stripping may not lead to immediate tree death, potentially outlasting vulture nests, which can deteriorate for other reasons like wind or vulture mortality (Vogel et al. 2014). To prevent bark-stripping, recent research has shown that wire-netting, which involves wrapping chicken-mesh around a tree's main stem, can be highly effective by improving the persistence of trees with a DBH of > 40 cm by reducing bark-stripping (Cook et al. 2023). As most vulture trees have a mean DBH of > 60 cm, wire-netting may be a highly effective method for protecting these trees. However, a longer-term study on the effects of bark-stripping on tree death, combined with monitoring vulture survival and breeding success, would provide more comprehensive insights.

In terms of scale, our results come from the APNR, where water is readily available to elephants. The APNR however, is part of a larger open system with the Great Limpopo Transfrontier Conservation Area, where elephants can move freely across resource and safety gradients (Smit et al. 2020). However, due to the provision of large numbers of artificial waterpoints, the APNR has been re-scaled to reflect the high levels of elephant impact which may be experienced in smaller protected areas where the spatial and temporal patterns of elephant effects on the environment are more difficult to regulate (Rushworth et al. 2018, Seloana et al. 2018, Linden et al. 2023). Elephant impact levels on the APNR's large trees may thus more closely reflect those of smaller, fenced protected areas versus what is experienced elsewhere within the GLTFCA.

Lastly, whilst our study focused on elephant impact to trees in which vultures nest, it is imperative that conservation efforts are also focused on the factors that negatively affect adult vulture survival, as this is critical for the survival of a long-lived bird species (Bamford et al. 2009, Monadjem et al. 2013). During our study period (2008–2020), a minimum of 803 vultures died from either poisoning (n = 785; 98%) or powerline-related (n = 18; 2%) mortalities in South Africa's Lowveld (low altitude savanna) region alone, which includes the APNR (the Endangered Wildlife Trust and Eskom (South Africa's Power Utility, unpubl. data). As a species which travels long distances across multiple countries and landscapes (Monadjem et al. 2013), an interdisciplinary approach that promotes adult vulture survival and the protection/availability of breeding sites, is required to protect and increase the numbers of vultures in South Africa (Botha et al. 2017, Thompson and Blackmore 2020). Furthermore, incorporating global positioning tags on vultures and analysing their movement patterns, alongside the study of elephant impact on their nesting trees and the recruitment rates of species favoured by vultures as nesting sites, could offer valuable insights into how increased levels of elephant activity may influence nest abandonment by vultures.

Conclusions

We present results from surveys in South Africa's APNR and an adjacent property where there are no elephants to investigate the impact that elephants are having on trees nested in by critically endangered vultures. We show that vultures in the APNR utilise a range of tree species and size classes across both riparian and woodland habitats, with riparian trees supporting nests that are significantly taller, have larger DBHs, and experience less elephant impact compared to woodland trees, which are more vulnerable to elephant activity. Focusing on *S. nigrescens*, the most abundant tree species containing vulture nests, our results suggest that the large trees (≥ 5 m in height or ≥ 40 cm in DBH; Shannon et al. 2008, Cook et al. 2023) nested in by vultures are most at threat to bark-stripping by elephants but are mostly too large to be toppled or stem snapped. However, elephants may be having a trimming effect on the tree heights available to vultures, and that nests are mostly found in the tallest *S. nigrescens* with the lowest elephant impact scores. We also highlight the impact that strong gusts of wind can have on nest persistence in trees. Further investigation into the thresholds of elephant impact on trees relative to the likelihood of vultures selecting them for nesting would significantly enhance these findings, particularly as elephant densities continue to increase in the APNR. This research could provide valuable insights for both vulture conservation and habitat management.

Acknowledgements – Core funding was provided by the US Fish and Wildlife Services and the Oak Foundation. Elephants Alive are thanked for providing historical data and for logistics support. We wish to thank the management and landowners of the Associated Private Nature Reserves for allowing us to conduct this research as well as for providing annual survey data. Air Force Base Hoedspruit are thanked for assistance with logistics and fieldwork. Christopher Rankin is thanked for statistical advice. Endangered Wildlife Trust and the South African Weather Service are thanked for providing us with vulture mortality and wind data respectively. Thank you to all volunteers who helped with tree surveys, particularly, Cheryl and Spencer Morrison, Daniel van der Vyver, Gabby Simmons, Johna Turna, Kassie Carstens, Michellene Munro, Prince Nkuna, Ronny Makukule, Sieglinde Rode, and Dr. Susanne Vogel.
Funding – Core funding was provided by the US Fish and Wildlife Services and the Oak Foundation. Elephants Alive are thanked

for providing historical data and for logistics support. We wish to thank the management and landowners of the Associated Private Nature Reserves for allowing us to conduct this research as well as for providing annual survey data. Air Force Base Hoedspruit are thanked for assistance with logistics and fieldwork. The Endangered Wildlife Trust and the South African Weather Service are thanked for providing us with vulture mortality and wind data respectively.
Permits – All appropriate ethics and other approvals were obtained for the research. A waiver approval for this research was granted by the Animal Ethics Research Committee of the University of the Witwatersrand (no. 18-01-2021-O).

Author contributions

Robin M. Cook: Conceptualization (supporting), Data curation (equal), Formal analysis (lead), Investigation (equal), Methodology (supporting), Project administration (equal), Writing - original draft (lead). **Edward T. F. Witkowski:** Conceptualization (supporting), Investigation (equal), Methodology (supporting), Supervision (lead), Visualization (equal), Writing - review and editing (lead). **Michelle D. Henley:** Conceptualization (lead), Data curation (equal), Funding acquisition (lead), Investigation (lead), Methodology (lead), Project administration (equal), Resources (lead), Supervision (lead), Visualization (lead), Writing - review and editing (lead).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01335.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m37pvmdcd (Cook et al. 2024).

References

Abraham, J. O., Goldberg, E. R., Botha, J. and Staver, A. C. 2021. Heterogeneity in African savanna elephant distributions and their impacts on trees in Kruger National Park, South Africa. – Ecol. Evol. 11: 5624–5634.

Adeola, A. M., Kruger, A., Elias Makgoale, T. and Ondego Botai, J. 2022. Observed trends and projections of temperature and precipitation in the Olifants River Catchment in South Africa. – PLoS One 17: e0271974.

Archibald, S., Twine, W., Mthabini, C. and Stevens, N. 2021. Browsing is a strong filter for savanna tree seedlings in their first growing season. – J. Ecol. 109: 3685–3698.

Asner, G. P., Vaughn, N., Smit, I. P. J. and Levick, S. 2016. Ecosystem-scale effects of megafauna in African savannas. – Ecography 39: 240–252.

Bamford, A. J., Monadjem, A. and Hardy, I. C. W. 2009. Nesting habitat preference of the African white-backed vulture *Gyps africanus* and the effects of anthropogenic disturbance. – Ibis 151: 51–62.

Barrett, A. and Brown, L. 2012. A novel method for estimating tree dimensions and calculating canopy volume using digital photography. – Afr. J. Range Forage Sci. 29: 153–156.

Birdlife International 2024. Species factsheet: white-backed vulture *Gyps africanus*. – https://datazone.birdlife.org/species/factsheet/white-backed-vulture-gyps-africanus.

Botha, A. J., Andevski, J., Bowden, C. G. R., Gudka, M., Safford, R., Tavares, J. and Williams, N. P. 2017. Multi-species action plan to conserve African-Eurasian vultures. – CMS Raptors MOU Technical Publication no. 5. CMS Technical Series no. 35. Coordinating Unit of the CMS Raptors MOU, Abu Dhabi, United Arab Emirates. pp. 1–164.

Chomba, C. and M'Simuko, E. 2013. Nesting patterns of raptors: white backed vulture (*Gyps africanus*) and African fish eagle (*Haliaeetus vocifer*), in Lochinvar National Park on the Kafue flats, Zambia. – Open J. Ecol. 3: 325–330.

Coetsee, C., Botha, J., Case, M. F., Manganyi, A. and Siebert, F. 2023. The hard lives of trees in African savanna – even without elephants. – Austral Ecol. 48: 532–551.

Coetzee, B. J., Engelbrecht, A. H., Joubert, S. C. J. and Retief, P. F. 1979. Elephant impact on *Sclerocarya caffra* trees in *Acacia nigrescens* tropical plains Thornveld of the Kruger National Park. – Koedoe 22: 39–60.

Cook, R. M., Witkowski, E. T. F. and Henley, M. D. 2023. Survival trends (2008–2020) of three tree species in response to elephant impact, environmental variation, and stem wire-netting protection in an African savanna. – Forest Ecol. Manage. 545: 121220.

Cook, R. M., Witkowski, E. T. F. and Henley, M. D. 2024. Data from: Impacts of African elephants and other environmental drivers on trees nested in by critically endangered white-backed vultures. – Dryad Digital Repository, https://doi.org/10.5061/dryad.m37pvmdcd.

Daboné, C., Buij, R., Oueda, A., Adjakpa, J. B., Guenda, W. and Weesie, P. D. 2019. Impact of human activities on the reproduction of hooded vultures *Necrosyrtes monachus* in Burkina Faso. – Ostrich 90: 53–61.

Das, A. A., Thaker, M., Coetsee, C., Slotow, R. and Vanak, A. T. 2022. The importance of history in understanding large tree mortality in African savannas. – Ecography 2022: e06012.

Eeden, R. van, Whitfield, D. P., Botha, A. and Amar, A. 2017. Ranging behaviour and habitat preferences of the martial eagle: implications for the conservation of a declining apex predator. – PLoS One 12: e0173956.

Fisher, L. D. and Lin, D. Y. 1999. Time-dependent covariates in the cox proportional-hazards regression model. – Annu. Rev. Public Health 20: 145–157.

GLTFCA 2022. Great Limpopo Transfrontier Conservation Area elephant management framework. – Technical report submitted to the by Conservation Outcomes Pretoria, South Africa. pp. 1–18.

Gordon, C. E., Greve, M., Henley, M., Bedetti, A., Allin, P. and Svenning, J.-C. 2023. Elephant rewilding affects landscape openness and fauna habitat across a 92-year period. – Ecol. Appl. 33: e2810.

Gould, M. S. 1993. The frequency of termite (Isoptera) damage to tree species in Namakutwa Forest, Tanzania. – Sociobiology 23: 189–198.

Greyling, M. D. 2004. Sex and age related distinctions in the feeding ecology of the African elephant. – Ph D thesis, Univ. of the Witwatersrand, South Africa.

Guldemond, R. A. R., Purdon, A. and Aarde, R. J. van 2017. A systematic review of elephant impact across Africa. – PLoS One 12: e0178935.
Helm, C. V. and Witkowski, E. T. F. 2012. Characterising wide spatial variation in population size structure of a keystone African savanna tree. – Forest Ecol. Manage. 263: 175–188.
Helm, C. V. and Witkowski, E. T. F. 2013. Continuing decline of a keystone tree species in the Kruger National Park, South Africa. – Afr. J. Ecol. 51: 270–279.
Helm, C. V., Scott, S. L. and Witkowski, E. T. F. 2011a. Reproductive potential and seed fate of *Sclerocarya birrea* subsp. *caffra* (marula) in the low altitude savannas of South Africa. – S. Afr. J. Bot. 77: 650–664.
Helm, C. V., Wilson, G., Midgley, J., Kruger, L. and Witkowski, E. T. F. 2011b. Investigating the vulnerability of an African savanna tree (*Sclerocarya birrea* ssp. *caffra*) to fire and herbivory. – Austral Ecol. 36: 964–973.
Henley, M. D. 2014. Report on elephant movements in relation to water and the effects of the 2012 floods within the Associated Private Nature Reserves. – Associated Private Nature Reserves: Elephants Alive, pp. 1–32.
Herbst, L. and Rautenbach, H. 2015. Climate change impacts on mean wind speeds in South Africa. – Clean Air J. 25: 17–17.
Hofmeyr, M. 2003. The spatial demography of elephant impacts on selected tree species in the Kruger National Park. – unpubl. report to the US Fish and Wildlife Services, Skukuza, South Africa, pp. 1–43.
Holm, S. 1979. A simple sequentially rejective multiple test procedure. – Scand. J. Stat. 6: 65–70.
Hood, I. A. 2006. The mycology of the Basidiomycetes. – Aciar Proc. 124: 34–34.
Jacobs, O. and Biggs, R. 2001. The effect of different fire treatments on the population structure and density of the marula, *Sclerocarya birrea* (A. Rich.) subsp. *caffra* (Sond.) kokwaro (Kokwaro & Gillet 1980) in the Kruger National Park. – Afr. J. Range Forage Sci. 18: 13–23.
Jenkins, A. R., Smallie, J. J. and Diamond, M. 2010. Avian collisions with power lines: a global review of causes and mitigation with a South African perspective. – Bird Conserv. Int. 20: 263–278.
Johnson, T. F. and Murn, C. 2023. Testing the importance of individual nest-site selection for a social and group-living vulture. – Afr. J. Ecol. 61: 6–13.
Kane, A. et al. 2022. Understanding continent-wide variation in vulture ranging behavior to assess feasibility of vulture safe zones in Africa: challenges and possibilities. – Biol. Conserv. 268: 109516.
Kemp, A. C. and Kemp, M. I. 1975. Observations on the white-backed vulture *Gyps africanus* in the Kruger National Park, with notes on other avian scavengers. – Koedoe 18: 51–68.
Kendall, C., Virani, M. Z., Kirui, P., Thomsett, S. and Githiru, M. 2012. Mechanisms of coexistence in vultures: understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. – Condor 114: 523–531.
Kendall, C. J., Rubenstein, D. I., Slater, P. L. and Monadjem, A. 2018. An assessment of tree availability as a possible cause of population declines in scavenging raptors. – J. Avian Biol. 49: e01497.
Khosa, A., Ndagurwa, H. G. T., Witkowski, E. T. F., Mutematemi, S. A., Mrewa, A. T., Zisadza, J., Nyenda, T. and Muvengwi, J. 2023. The impact of elephants (*Loxodonta africana*) on the baobab (*Adansonia digitata*) in a semi-arid savanna. – Global Ecol. Conserv. 46: e02556.
Kleinbaum, D. G. and Klein, M. 2012. Evaluating the proportional hazards assumption. – In: Kleinbaum, D. G. and Klein, M. (eds), Survival analysis: a self-learning text. – Statistics for Biology and Health. Springer, pp. 161–200.
Levick, S. R. and Asner, G. P. 2013. The rate and spatial pattern of treefall in a savanna landscape. – Biol. Conserv. 157: 121–127.
Linden, E., Rittenhouse, C. D., Peel, M. J. S., Ortega, I. M. and Smit, I. P. J. 2023. Vegetation changes following large-scale fence removal across a protected area network within the Kruger to Canyons Biosphere Reserve, South Africa. – Ecosystems 26: 768–783.
Linstrom, A. 2018. Ngwenya Lodge waste water treatment works (new location): wetland and riparian zone identification and description. – Wet-Earth Eco-Specs, pp. 1–55.
Marr, S., Mohlala, T. and Swemmer, A. 2017. The ecological integrity of the lower Olifants River, Limpopo province, South Africa: 2009–2015 – Part B: tributaries of the Olifants River. – Afr. J. Aquat. Sci. 42: 181–190.
Martínez, J. E., Jiménez-Franco, M. V., Zuberogoitia, I., León-Ortega, M. and Calvo, J. F. 2013. Assessing the short-term effects of an extreme storm on Mediterranean forest raptors. – Acta Oecol. 48: 47–53.
Mashele, N. M., Thompson, L. J. and Downs, C. T. 2021. Traditional health practitioners' and other community members' perceptions of vultures in the Kruger to Canyons Biosphere Region, South Africa. – J. Raptor Res. 55: 340–358.
Midgley, J. J., Lawes, M. J. and Chamaillé-Jammes, S. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. – Aust. J. Bot. 58: 1–11.
Miller, M. F. 1995. Acacia seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. – Afr. J. Ecol. 33: 194–210.
Mitchell, S. J. 2013. Wind as a natural disturbance agent in forests: a synthesis. – Forestry 86: 147–157.
Moe, S. R., Rutina, L. P., Hytteborn, H. and Du Toit, J. T. 2009. What controls woodland regeneration after elephants have killed the big trees? – J. Appl. Ecol. 46: 223–230.
Monadjem, A. and Garcelon, D. K. 2005. Nesting distribution of vultures in relation to land use in Swaziland. – Biodivers. Conserv. 14: 2079–2093.
Monadjem, A., Botha, A. and Murn, C. 2013. Survival of the African white-backed vulture *Gyps africanus* in north-eastern South Africa. – Afr. J. Ecol. 51: 87–93.
Mucina, L. and Rutherford, M. C. 2006. The vegetation of South Africa, Lesotho and Swaziland. – Strelitzia.
Murn, C. and Anderson, M. D. 2008. Activity patterns of African white-backed vultures *Gyps africanus* in relation to different land-use practices and food availability. – Ostrich 79: 191–198.
N'Dri, A. B., Gignoux, J., Konaté, S., Dembélé, A. and Aïdara, D. 2011. Origin of trunk damage in West African savanna trees: the interaction of fire and termites. – J. Trop. Ecol. 27: 269–278.
O'Connor, T. G., Goodman, P. S. and Clegg, B. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. – Biol. Conserv. 136: 329–345.
Ogada, D. L., Keesing, F. and Virani, M. Z. 2012. Dropping dead: causes and consequences of vulture population declines worldwide. – Ann. N.Y. Acad. Sci. 1249: 57–71.
Ogada, D., Shaw, P., Beyers, R. L., Buij, R., Murn, C., Thiollay, J. M., Beale, C. M., Holdo, R. M., Pomeroy, D., Baker, N., Krüger, S. C., Botha, A., Virani, M. Z., Monadjem, A. and Sinclair, A. R. E. 2016. Another continental vulture crisis: Africa's vultures collapsing toward extinction. – Conserv. Lett. 9: 89–97.

Owen-Smith, R. N. 1988. Megaherbivores: the influence of very large body size on ecology. – Cambridge Univ. Press.
Palmer, T. M. and Brody, A. K. 2013. Enough is enough: the effects of symbiotic ant abundance on herbivory, growth, and reproduction in an African *Acacia*. – Ecology 94: 683–691.
Parker, A. H. and Witkowski, E. T. F. 1999. Long-term impacts of abundant perennial water provision for game on herbaceous vegetation in a semi-arid African savanna woodland. – J. Arid Environ. 41: 309–321.
Peters, N. M., Kendall, C. J., Davies, J. G., Bracebridge, C., Nicholas, A., Mgumba, M. P. and Beale, C. M. 2023. Identifying priority locations to protect a wide-ranging endangered species. – Biol. Conserv. 277: 109828.
Rushworth, I. and Krüger, S. 2014. Wind farms threaten southern Africa's cliff-nesting vultures. – Ostrich 85: 13–23.
Rushworth, I. A., Druce, D., Craigie, J. and Coverdale, B. 2018. Vulnerability of vulture populations to elephant impacts in KwaZulu-Natal. – Bothalia 48: 1–10.
Scholes, R. J. and Archer, S. R. 1997. Tree-grass interactions in savannas. – Annu. Rev. Ecol. Syst. 28: 517–544.
Seloana, M. Q., Jordaan, J. J., Potgieter, M. J. and Kruger, J. W. 2018. Feeding patterns of elephants at the Atherstone Collaborative Nature Reserve. – Afr. J. Ecol. 56: 445–454.
Seymour, C. and Joseph, G. 2019. Ecology of smaller animals associated with savanna woody plants. – In: Savanna woody plants and large herbivores. John Wiley & Sons, Ltd, pp. 181–211, https://onlinelibrary.wiley.com/doi/abs/10.1002/9781119081111.ch7.
Shannon, G., Druce, D. J., Page, B. R., Eckhardt, H. C., Grant, R. and Slotow, R. 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. – J. Trop. Ecol. 24: 281–289.
Smit, I. P. J., Peel, M. J. S., Ferreira, S. M., Greaver, C. and Pienaar, D. J. 2020. Megaherbivore response to droughts under different management regimes: lessons from a large African savanna. – Afr. J. Range Forage Sci. 37: 65–80.
Swemmer, A. M., Nippert, J. B. and O'Connor, T. G. 2023. The effects of floods, droughts and elephants on riparian tree mortality in a semi-arid savanna. – Forest Ecol. Manage. 545: 121264.
Teren, G., Owen-Smith, N. and Erasmus, B. F. N. 2018. Elephant-mediated compositional changes in riparian canopy trees over more than two decades in northern Botswana. – J. Veg. Sci. 29: 585–595.
Therneau, T. M. 2023. – Coxme: mixed effects Cox models. R package ver. 2.2-18. https://CRAN.R-project.org/package=coxme.
Therneau, T. M. 2024. A package for survival analysis in R. – R Package ver. 3.7-0, https://CRAN.R-project.org/package=survival.
Thompson, K. E., Ford, A., Esteban, G., Poupard, A., Zoon, K. and Pettorelli, N. 2022. Impacts of African savannah elephants (*Loxodonta africana*) on tall trees and their recovery within a small, fenced reserve in South Africa. – Afr. J. Ecol. 60: 357–366.
Thompson, L. J. and Blackmore, A. C. 2020. A brief review of the legal protection of vultures in South Africa. – Ostrich 91: 1–12.
Thompson, L. J., Krüger, S. C., Coverdale, B. M., Shaffer, L. J., Ottinger, M. A., Davies, J. P., Daboné, C., Kibuule, M., Cherkaoui, S. I., Garbett, R. A., Phipps, W. L., Buechley, E. R., Godino Ruiz, A., Lecoq, M., Carneiro, C., Harrell, R. M., Gore, M. L. and Bowerman, W. W. 2021. Assessing African vultures as biomonitors and umbrella species. – Front. Conserv. Sci. 2021: e729025.
Thornley, R., Spencer, M., Zitzer, H. R. and Parr, C. L. 2020. Woody vegetation damage by the African elephant during severe drought at Pongola Game Reserve, South Africa. – Afr. J. Ecol. 58: 658–673.
Turner, J., Owen-Smith, N., Kruger, L., Wigley-Coetsee, C. and O'Connor, T. G. 2022. Shifting patch dynamics of floodplain woodlands in an arid savanna region: effects of soil form, flooding and large herbivores. – S. Afr. J. Bot. 151: 866–875.
Van den Heever, L., Thompson, L. J., Bowerman, W. W., Smit-Robinson, H., Shaffer, L. J., Harrell, R. M. and Ottinger, M. A. 2021. Reviewing the role of vultures at the human-wildlife-livestock disease interface: an African perspective. – J. Raptor Res. 55: 311–327.
Van Langevelde, F., Sianga, K., van Telgen, M., Vrooman, M. and Fynn, R. W. S. 2017. Spatial refuges buffer landscapes against homogenisation and degradation by large herbivore populations and facilitate vegetation heterogeneity. – Koedoe 59: 1–13.
Virani, M., Kirui, P., Monadjem, A., Thomsett, S. and Githiru, M. 2010. Nesting status of African white-backed vultures *Gyps africanus* in the Masai Mara National Reserve, Kenya. – Ostrich 81: 205–209.
Vogel, S. M., Henley, M. D., Rode, S. C., van de Vyver, D., Meares, K. F., Simmons, G. and de Boer, W. F. 2014. Elephant (*Loxodonta africana*) impact on trees used by nesting vultures and raptors in South Africa. – Afr. J. Ecol. 52: 458–465.
Walker, S. H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. – S. Afr. J. Wildl. Res. 6: 1–32.
Watson, L. H., Cameron, M. J. and Iifo, F. 2020. Elephant herbivory of knob-thorn (*Senegalia nigrescens*) and ivory palm (*Hyphaene petersiana*) in Bwabwata National Park, Caprivi, Namibia: the role of ivory palm as a biotic refuge. – Afr. J. Ecol. 58: 14–22.
West, S. G., Aiken, L. S., Wu, W. and Taylor, A. B. 2007. Multiple regression: applications of the basics and beyond in personality research. – In: Robins, R. W., Fraley, R. C. and Krueger, R. F. (eds), Handbook of research methods in personality psychology. The Guilford Press, pp. 573–601.
Wigley, B. J., Coetsee, C., Kruger, L. M., Ratnam, J. and Sankaran, M. 2019. Ants, fire, and bark traits affect how African savanna trees recover following damage. – Biotropica 51: 682–691.
Witkowski, E. T. F. 1983. Ecology of the Klaserie Private Nature Reserve. – MSc thesis, Univ. of the Witwatersrand, Johannesburg, South Africa.
Wolter, K. and Howard, A. 2019. Cape, African white-backed and hooded vulture breeding surveys. – VulPro: 1–9.