



Effect of drought on wildlife activity at artificial waterholes

Ngaatendwe Ndachena^a, Marjolein E.M. Toorians^a, Maxwell J. Farrell^b, Danny Govender^{c,d}, T. Jonathan Davies^{a,e,f,*}

^a Department of Botany, University of British Columbia, Canada

^b Medical Research Council—University of Glasgow Centre for Virus Research, Glasgow, UK

^c SANParks Scientific Services, South Africa

^d University of Pretoria, South Africa

^e Department of Forest & Conservation Sciences, University of British Columbia, Canada

^f African Centre for DNA Barcoding, University of Johannesburg, South Africa

ARTICLE INFO

Keywords:

Animal behaviour
Camera trap
Climate change
Conservation
Drought
Temporal overlap

ABSTRACT

Across southern Africa artificial waterholes have been introduced into many national parks to reduce the pressure of water scarcity on animals during drought. However, their introduction can shift ecological dynamics, and many artificial waterholes are now being removed. As global temperatures rise, droughts are predicted to become more frequent and more severe. Whether to retain or remove artificial waterholes thus presents a management dilemma. Here, we examine the effect of an extreme drought on artificial waterhole use in the Kruger National Park, South Africa. Comparing camera trap data collected during a one-in-twenty year drought with observation from a non-drought year, we quantify shifts in waterhole visitation patterns between years. The majority of the species show differences in waterhole use between drought and non-drought years. Species showing the largest temporal shifts include kudu and white rhinoceros, whereas elephants and warthogs show little change between years. Temporal overlaps between species pairs were also highly shifted, with the majority of species overlapping more in drought years, although some (e.g. buffalo and impala) show the opposite trend. Asynchronous shifts in species daily activity cycle may have cascading impacts on interspecific competition, predator-prey interactions, and multi-host disease dynamics. Our study illustrates how the interaction between drought and management choices to mitigate impacts of climate change may have complex and unforeseen ecological consequences. We show that, during drought, artificial waterholes are visited more frequently, likely increasing the frequency of interspecific interactions, including between ungulate herbivores and their predators, and elevating risk of disease spillover.

1. Introduction

Savannas are one of the world's largest terrestrial biomes covering an area of approximately 33 million km² and today over 50 % of the African continent is comprised of savanna (Ramankutty and Foley, 1999). While the savanna biome in southern Africa is relatively young (perhaps no more than 3–4 million years) (Maurin et al., 2014; Davies et al., 2020), it supports a high diversity of large (mega) herbivores including elephants, rhinoceros and giraffe (Janis et al., 2000), many of which are now threatened with extinction (Craigie et al., 2010; Di Marco et al., 2014).

The savanna biome experiences intense interannual and seasonal fluctuations in rainfall which are accompanied by a wide range of

temperatures. Dry years tend to be characterised by higher temperatures and increased heat waves as well as low rainfall (Zambatis and Biggs, 1995). This climate variability impacts the year-round availability of water and results in frequent droughts (Van Wyk, 2001). Drought may have both direct and indirect effects on the survival of large herbivores in savannas (Walker et al., 1987). Water scarcity can promote the aggregation and transmission of parasites, with exposure amplified in drier periods (Titcomb et al., 2021). Large herbivores, such as elephants, may accumulate near water sources, depleting the surrounding vegetation, which can lead to increased mortality rates through starvation (Wato et al., 2016). In drought years, wildlife mortality is primarily a consequence of lack of forage and not lack of water (Smit et al., 2020).

The Kruger National Park (KNP) in South Africa was originally

* Corresponding author at: Department of Botany, University of British Columbia, Canada.

E-mail address: j.davies@ubc.ca (T.J. Davies).

<https://doi.org/10.1016/j.biocon.2025.111370>

Received 12 October 2024; Received in revised form 3 July 2025; Accepted 10 July 2025

Available online 21 July 2025

0006-3207/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

founded to maintain game numbers depleted by hunting and the great rinderpest epidemic of 1896 (Pienaar et al., 1997). Beginning in the 1930s, artificial waterholes were introduced to stabilize surface water availability (Van Wyk, 2001). From the 1930s through to the 1990s approximately 400 artificial water points were established in the park (Smit et al., 2020). These artificial waterholes provide water during drought periods, helping conserve game numbers, spread animals over the park and prevent animals from migrating out of the KNP (Pienaar et al., 1997). Historically, the introduction of waterholes was considered to have had a positive impact, including increasing numbers of (water-dependent) herbivore species such as zebra, elephant and impala (Van Wyk, 2001; Smit et al., 2007). Additionally, they putatively acted to reduce competition and impacts of over-grazing along rivers during the dry season, with the added benefit of attracting animals for tourist viewing (Pienaar et al., 1997).

Artificial waterholes are now also recognised to have had negative effects on the ecosystem (Smit et al., 2007; Smit et al., 2020, see also review by Perkins, 2020). The increase in drought-intolerant species came at the expense of other large and mid-sized herbivores, such as sable, roan and tsessebe antelope, which decreased in numbers due to increased competition for food (Smit et al., 2007). The introduction of artificial waterholes is also thought to have brought about changes in animal behaviour. In the dry season, grazers tend to relocate nearer artificial waterholes, and browsers and mixed feeders are found more at either artificial waterholes or near rivers (Smit et al., 2007). As the dry season advances animals increasingly aggregate at artificial sites. These shifts in space use may have cascading consequences for both inter-specific competition (Smit et al., 2007) and predator-prey interactions (Thrash et al., 1995; Valeix et al., 2009a, 2009b). In addition, the increased aggregation of species at waterholes provides a greater opportunity for disease spillover (Farrell et al., 2022), for example, bovine tuberculosis (bTB), for which buffalo are the reservoir host, was first detected in rhinoceros immediately following the 2015/2016 drought (Dwyer et al., 2022). From the mid-1990s the KNP reversed its water provisioning strategy (Pienaar et al., 1997), and started removing artificial waterholes from the park (Smit et al., 2020).

The decisions to establish and then subsequently remove waterholes was part of the Strategic Adaptive Management (SAM) framework adopted by the park (Smit et al., 2020). This framework recommends actions based on the best available information, even if information is incomplete (see Roux and Foxcroft, 2011). With ongoing anthropogenic climate change, simply removing artificial waterhole sites will not return the park to a state that predates their establishment. Yet as global temperatures continue to rise, more frequent and more severe droughts are expected (Engelbrecht et al., 2015), and thus the ecological impacts of artificial waterholes in the park will likely be further amplified. A more complete understanding of how water scarcity and the introduction of artificial waterholes alter ecological dynamics will be critical for informing management decisions and policies in the KNP (Smit et al., 2020) and actions for mitigating future impacts of climate change (Weeber et al., 2020).

Here, we explore the effects of artificial waterholes on wildlife in the KNP by comparing waterhole use between two years differing in water availability, 2015 and 2022. The former was a major drought year in the KNP with extremely low rainfall (annual total 242 mm), especially during the summer (Malherbe et al., 2020). The 2015/2016 drought was exceptional, perhaps a one in twenty year event, and comparable to extreme droughts recorded in 1982/1983 and 1991/1992 (Malherbe et al., 2016) for which mass die-offs were observed in buffalo and hippo (Smit et al., 2020). The 2022 season was an above average rainfall year (567 mm compared to the long term historical average of 557 mm; <https://www.sanparks.org/conservation/scientific-services/data-information-resources/kruger-climate-rainfall>).

Using site occupancy data collected with camera traps in 2015 (Farrell et al., 2022) and 2022 (Toorians et al. unpublished) to describe species' daily waterhole visitation patterns (Ridout and Linkie, 2009),

we examine how water availability alters ecological interactions, replicating observations across species and waterhole sites. We test how the extreme drought in 2015 (1) influenced species aggregation at waterhole sites, (2) shifted individual species' daily waterhole visitation patterns, and (3) altered species interactions.

In general, we predict that the reduced availability of water in natural pans and rivers during the drought year would increase artificial waterhole use, with drought intolerant and water-dependent species showing the greater increase in waterhole visitation rates (Valeix, 2011). However, we do not have strong a priori predictions on temporal shifts in daily waterhole visitation patterns between the drought and non-drought years as species may have been subject to multiple competing pressures. For example, shifting to earlier in the day may allow animals to avoid the midday heat (Ayeni, 1975), whereas shifting to later in the day, when temperatures were warmer, may provide animals with an opportunity to reduce heat stress by wallowing (Ayeni, 1975). Because the increased concentration of animals at waterholes in the drought year might have been a draw to predators, such as lions, some prey species might additionally alter waterhole visitation patterns to minimise predation risk, shifting to later in the day when predators are generally less active (Thrash et al., 1995; Valeix et al., 2009a, 2009b; Hayward and Hayward, 2012). A trend towards an overall increasing frequency of waterhole visitation would tend to increase species co-occurrences at waterholes; however, we might expect this to be less apparent between predator and prey species where there is active avoidance by the latter.

2. Methods

We used camera trap data collected from the Kruger National Park (KNP) in 2015 (June and July) and 2022 (June) (Farrell et al., 2022; Toorians et al., unpublished) to describe waterhole visitation patterns by large mammals. Model Bushnell Aggressor Trophy Cam HD Low-Glow cameras were placed in metal cases and attached to the concrete ball-valve housing, on trees, or on poles at artificial waterholes. Cameras were set to record photographs at five-minute intervals and when motion was detected with a minimum one-minute interval between photographs. For this analysis, only the time-lapse data were used. Each photograph was manually annotated to record the abundance of each species in direct contact with or next to the waterhole. Animals captured in the background of the photographs were excluded. For further detail see Farrell et al. (2022). These data provide us with a temporal record of species at waterholes, including patterns of spatial and temporal co-occurrence, i.e. the relative frequency species were recorded at the same location and time of day, respectively.

In 2015, images were recorded from six artificial waterhole sites in the southern half of the park (De Laporte [DLP], Kwaggaspan [KWA] and N'waswitshaka [NWA], Hoyo Hoyo [HOY], Ngotso North [NGN] and Nyamahri [NYA], and in 2022 images were recorded from five sites (DLP, KWA, NWA, Gomondwane [GOM], and Duke [DUKE]), with three sites (DLP, KWA and NWA) overlapping between years (Fig. 1). For all subsequent analyses, we explored waterhole visitation patterns at three scales: first, at each overlapping site (DLP, KWA, and NWA) separately; second, across the three overlapping sites (DLP, KWA, and NWA) together; and third, all artificial waterhole sites combined (DLP, DUKE, GOM, HOY, KWA, NGN, NWA, and NYA). The number of individuals per species present at the waterhole was recorded. Overlap coefficients reported in the main text are for all artificial sites combined, matching results for the individual sites and the three overlapping sites combined are reported in the appendix.

The 2015 drought was a rare event, and thus it is not possible to collect replicated data within a reasonable timeframe; however, as evidenced by the multiple studies showing species' behavioural changes during the COVID-19 lockdown (Bates et al., 2021), rare events can still provide valuable information, and we gain statistical strength from replicate observations across species and waterhole sites.

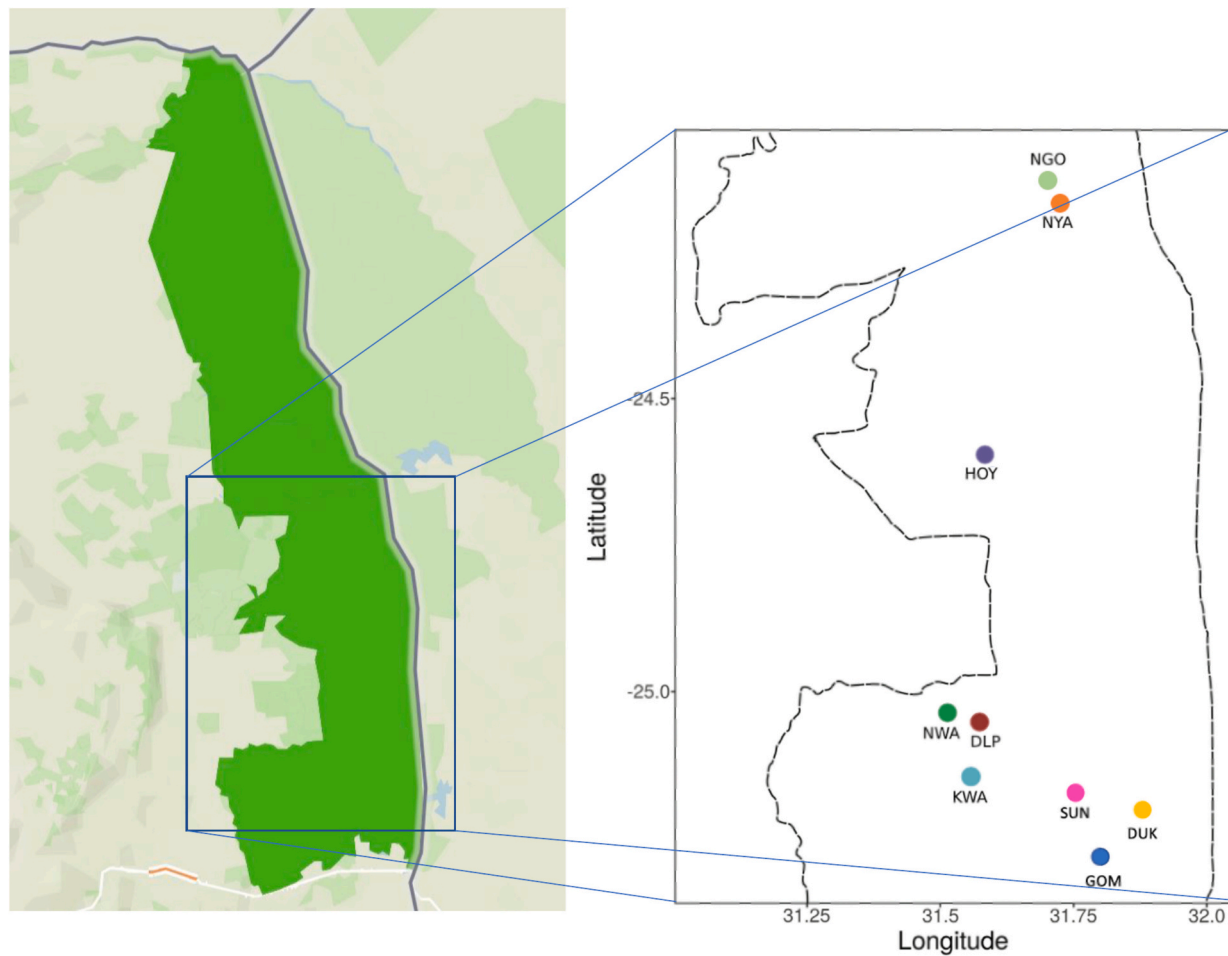


Fig. 1. Map of Kruger National Park showing camera trap locations. Park boundary shown on the left in green, enlarged inset indicating location of waterhole at which camera trap data was collected. In 2015, images were recorded from six sites: De Laporte [DLP], Kwaggaspan [KWA] and N’waswitshaka [NWA], Hoyo Hoyo [HOY], Ngotso North [NGN] and Nyamahri [NYA]. In 2022, images were recorded from five sites: DLP, KWA, NWA, Gomondwane [GOM], and Duke [DUKE]). Base map for the Protected Area Profile for Kruger National Park obtained from the World Database on Protected Areas, May 2025. Available at: www.protectedplanet.net. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.1. Temporal overlap and interspecific interaction strengths

We examined temporal change in community composition between the years 2015 and 2022 for each of the overlapping sites shared between years (DLP, KWA and NWA). Using presence/absence data and the Jaccard Index, we computed the pairwise dissimilarity for each site between 2015 and 2022, considering the turnover and nestedness components of temporal change. Calculations were performed using the R-package Betapart (Baselga et al., 2023), index.family = “jaccard” and indices beta.JTU (turnover) and beta.JNE (nestedness).

2.2. Shifts in daily waterhole visitation patterns

We examined changes in visitation patterns for the following 11 species: impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), elephant (*Loxodonta africana*), greater kudu (*Tragelaphus strepsiceros*), white rhinoceros (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), zebra (*Equus quagga*), spotted hyena (*Crocuta Crocuta*), lion (*Panthera leo*), warthog (*Phacochoerus africanus*), and chacma baboon (*Papio ursinus*). We focus on this set of species as they were well represented in the camera trap images between years (impala, giraffe, elephant and zebra had the greatest number of photographs), and are either species of conservation concern (white rhinoceros) or disease risk (buffalo), and because it allowed us to explore shifting predator-prey interactions (lion and hyena).

We described each species’ use of waterholes from the camera trap data, converting visitation times (recorded as hour-minute-second) into radians ($1 \text{ min} = 2.9 \cdot 10^{-4} \text{ rad}$), separately for 2015 and 2022. We then estimated a temporal overlap coefficient (\widehat{O}_{est}) of overlapping densities (density kernels – see below) between years using the R-package Overlap (v0.3.3; Ridout and Linkie, 2009), which uses kernel density estimates that sort the data times into two functions, $f(t)$ and $g(t)$, the surfaces of the estimated density kernels of the same species in the different years. We use the model output, which is calculated from vectors of densities that are estimated at T equally spaced intervals (Ridout and Linkie, 2009) to derive \widehat{O}_{est} :

$$\widehat{O}_{est} = 2\pi / T \sum_{i=1}^T \min(\widehat{f}(t_i), \widehat{g}(t_i))$$

The temporal overlap coefficient (\widehat{O}_{est}) quantifies the relative time-span two sets of temporal observations (here summarised over a 24-hour period) overlap, for example, observations of the time of day a species is recorded at a waterhole between years or observations for two separate species in the same calendar window (see below).

To evaluate whether species shifted their waterhole visitation patterns to earlier or later in the day in the drought year, we estimated whether the temporal overlap between years differed from null expectations of no change by comparing \widehat{O}_{est} to a null distribution of overlap

constructed by shuffling year among photographs and recalculating the overlap, O_{rand} . We calculated the probability of departure from the null (p) by summing the number of occasions when $\widehat{O}_{est} > O_{rand}$, and dividing by the number of null simulations ($n = 1000$):

$$p = \frac{\sum (\widehat{O}_{est} > O_{rand})}{n}$$

Here, p represents the relative frequency O_{rand} was smaller than the estimated overlap, \widehat{O}_{est} . Assuming a two-tailed test at $\alpha = 0.05$, we interpret $0.025 < p < 0.975$ to indicate a significant departure from the null.

2.3. Temporal overlap

To explore shifts in temporal overlap between species pairs across years, we calculated the temporal overlap coefficient for every species pair in each year and then subtracted the overlap coefficient for 2022 ($O_{est2022}$) from the overlap coefficient for 2015 ($O_{est2015}$):

$$\Delta \widehat{O}_{est} = O_{est2015} - O_{est2022}$$

Positive values of $\Delta \widehat{O}_{est}$ indicate that the estimated overlap coefficient in 2015 was larger than the estimated overlap coefficient for 2022, and negative values of $\Delta \widehat{O}_{est}$ indicate that the temporal overlap coefficient in 2015 was less than that for 2022.

To evaluate whether shifts in estimated temporal overlap between years ($\Delta \widehat{O}_{est}$) differed from null expectations, we again generated a null distribution of temporal species co-occurrences by shuffling year among photographs. We then calculated the overlap coefficients between species pairs using overlap estimates from the null randomizations ($O_{rand,pair}$). Using 2015 as our baseline, we subtracted our random overlap coefficient ($O_{rand,pair}$) from the estimated overlap of that species pair in 2015 ($O_{est2015}$), to generate a null expectation ($\Delta O_{rand,pair}$) of difference in overlap between years keeping the total number of images constant.

$$\Delta O_{rand,pair} = O_{est2015} - (O_{rand,pair})$$

To calculate a test statistic, we then counted the number of times the random overlap difference ($\Delta O_{rand,pair}$) was smaller than the estimated overlap difference between 2015 and 2022 ($\Delta \widehat{O}_{est}$), and dividing by the number of null simulations ($n = 1000$), as described above:

$$p = \frac{\sum (\Delta \widehat{O}_{est} > \Delta O_{rand,pair})}{n}$$

Here, p represents the relative frequency that $\Delta O_{rand,pair}$ was smaller than the estimated difference in overlap, $\Delta \widehat{O}_{est}$. Assuming a two-tailed test with $\alpha = 0.05$, we interpret $0.025 < p < 0.975$ to indicate a significant departure from the null.

2.4. Temporal overlap and spatial co-occurrence

Finally, we examined whether greater estimates of temporal overlap for a species pair, as calculated above, translated into greater probability of seeing that species pairs in the same photograph (spatial co-occurrence). For each year separately, we therefore calculated the observed spatial co-occurrence ($O_{spatial}$) by dividing the number of photographs a species pair was seen together ($N_{together}$) by the total number of photographs of the species that was seen less often (N_{single}):

$$O_{spatial} = N_{together} / N_{single}$$

These values range from 0 to 1 (0 = the species pair was not seen together in any photographs, and 1 = the species pair was always seen together when the less common observed species was photographed).

We then compared these values to the estimated temporal overlap coefficients from 2015 ($\widehat{O}_{est2015}$) and 2022 ($\widehat{O}_{est2022}$).

3. Results

We analysed a total of 11,742 camera images (see Fig. 2 for example photographs) across years ($n = 11,244$ and 498 for 2015 and 2022, respectively), capturing 26 species, with greater richness of species in 2015 ($n = 25$ versus 23 for 2015 and 2022, respectively; Table 1). Some species, such as impala, elephant and buffalo were relatively frequent visitors in both years, whereas other species, such as zebra and warthog, were commonly seen in 2015 but only rarely observed in 2022 (Table S1).

3.1. Changes in species composition

We explored temporal change in community composition between the years 2015 and 2022 for each of the overlapping sites shared between years (DLP, KWA and NWA), examining components of turnover (β TJU) and nestedness (β JNE) (Table 1). Nestedness captures differences in species richness between observations, with the expectation that species recorded at waterholes in non-drought years would be a nested subset of the species recorded visiting waterholes in the drought year due to generally higher visitation rates in the drought year. We found evidence for high nestedness, with 2015 being the more species rich, as predicted, while there was generally low turnover in species composition (β JNU = 0.00 for DLP and KWA; see Table 1). For these sites, the species observed in 2022 were a nested subset of the species observed in 2015 (β JNE = 0.40 and β JNE = 0.50 for the sites DLP and KWA, respectively). For the third site shared between years, NWA, turnover was greater than nestedness (β TJU = 0.57 and β JNE = 0.06), indicating substantial change in species identities at this site between years (Table 1).

3.2. Changes in daily waterhole visitation patterns

We found an overall trend for lower overlap (\widehat{O}_{est}) in waterhole visitation patterns between years than expected from the null generated by randomising year across photographs (Fig. 3 and Table S1). This deviation was significant (two-tailed test, $p < 0.025$) for several species, including impala, kudu, buffalo, hyena, white rhinoceros and baboon. For example, impala, for which we had the greatest number of images ($n = 1075$, all sites combined), had an estimated temporal overlap coefficient of 0.73 between 2015 and 2022, whereas the expected overlap from randomisations was 0.90 (Table S1). In 2015, the drought year, the majority of recorded visits to waterholes by impala were before noon, by contrast, in 2022 impala were observed at waterholes from 6 am to 6 pm (Fig. 3). Although there were fewer photographs of rhinoceros ($n = 41$), the departure from null expectations was still highly significant ($p = 0.001$). The 2015 daily waterhole visitation patterns again had a peakier distribution, with most visitations in the late afternoon, while waterhole visits were generally sparser in 2022, and with a greater frequency of visits in late evenings and early mornings (Fig. 3).

While warthog and lion both appeared to show greater overlap than the mean from randomisations (Table S1), these estimates were derived from only 105 and 10 images respectively, and the difference between estimated overlap and null expectations were not statistically significant ($p > 0.025$, Table S1).

For species with sufficient number of observations to calculate density distributions, overlap trends were consistent when we restricted our analyses to the three sites shared between years (DLP, KWA and NWA; Table S3) and when examining each of these sites individually (Tables S4, S5 and S6). In some cases, lower sample size reduced significance (e.g. changes in overlap were no longer significantly different from the null for buffalo and hyena in DLP; Table S4); however, trends

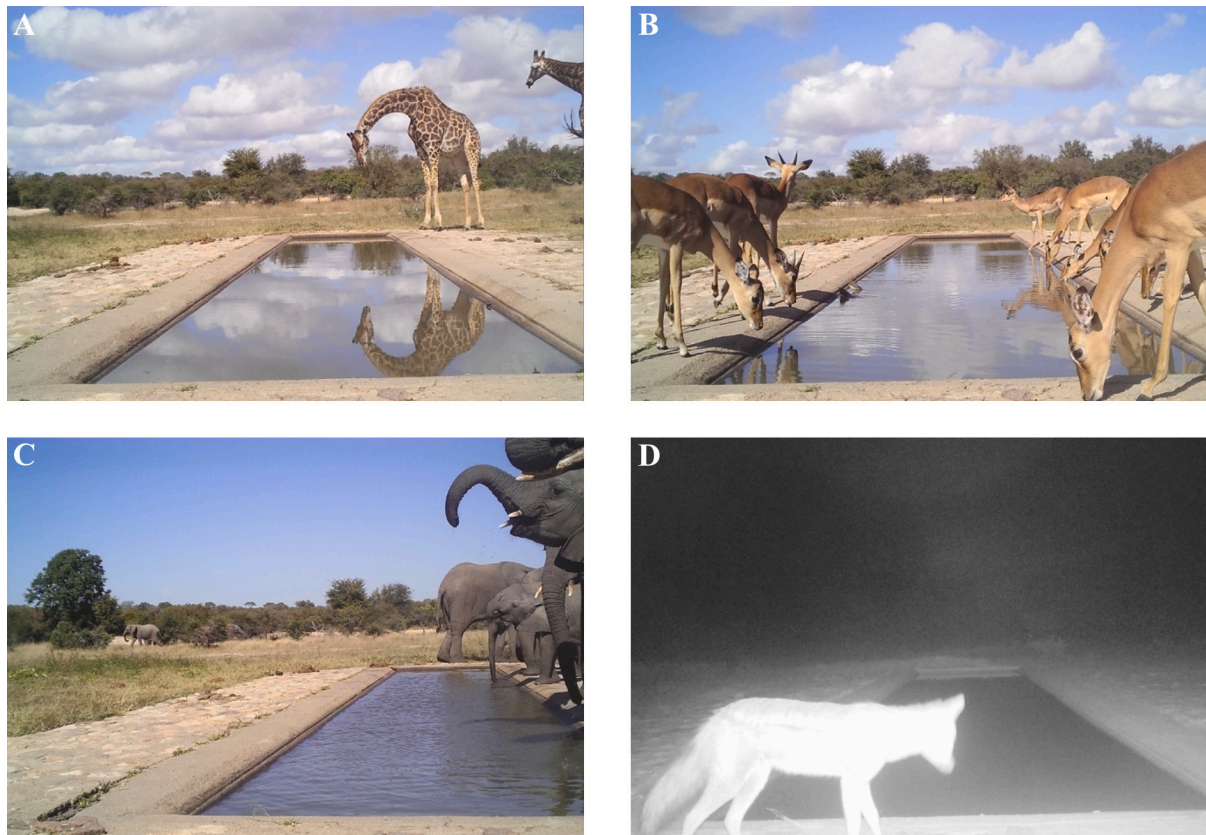


Fig. 2. Example photographs from camera traps. Example photographs (A–D) from a camera trap situated at N’waswitshaka capturing various species visitation patterns across different times of the day.

Table 1
Change in species composition between years.

Species richness		Site	Turnover (β JTU)	Nestedness (β JNE)
2015	2022	DLP	0.00	0.40
25 (19)	23 (18)	KWA	0.00	0.50
		NWA	0.57	0.06

The first two columns show species richness for all artificial sites with species richness for the overlapping sites in parentheses in 2015 and 2022, respectively. The next three columns show a comparison of beta diversity components, turnover (β JTU) and nestedness (β JNE), for each of the overlapping sites between the years 2015 and 2022.

suggesting lower temporal overlap than the mean from randomisations were consistent in direction. Elephants were one notable exception. Although elephants did not show a significant shift in activity cycles between years when sites were combined (Tables S1 and S3), when sites were analysed separately, elephants showed significant shifts towards lower than expected temporal overlap between years across sites (Tables S4, S5 and S6).

3.3. Temporal overlap and interspecific interaction strengths

We found evidence for species pairs both increasing and decreasing in their temporal overlap ($\Delta \widehat{O}_{est}$) between 2015 and 2022, but shifts towards greater temporal overlap in the drought year dominated (Fig. 4). In our analysis, positive values (Fig. 4, green) indicate that the estimated overlap coefficient in 2015 ($\widehat{O}_{est2015}$) was larger than the estimated overlap coefficient for 2022 ($\widehat{O}_{est2022}$) for that species pair, while negative values (Fig. 4, purple) indicate that the temporal overlap coefficient in 2015 was less than that for 2022. For example, the overlap

coefficient for giraffe and kudu, both large ungulate browsers, was 0.82 in 2015, but these two species did not temporally overlap in 2022 (Fig. 4 and Table S2). We also observed a significant decrease in temporal overlap in the non-drought year for species pairs that represent potential predator-prey interactions, such as between giraffe and lion ($\widehat{O}_{est2015} = 0.13$ versus $\widehat{O}_{est2022} = 0.00$, $p < 0.001$; see Fig. 4 and Table S2). However, temporal overlap between kudu and hyena was greater in the non-drought year than the drought year ($\widehat{O}_{est2022} = 0.81$ versus $\widehat{O}_{est2015} = 0.03$, $p < 0.001$; Fig. 4 and Table S2), due to a shift by kudu towards drinking nocturnally in the non-drought year.

We found consistent trends when evaluating the three sites shared across years, with the vast majority of significant shifts indicating lower temporal overlap between species pairs in the non-drought year (Fig. S1, Table S7). In almost all cases, when data were sufficient for statistical significance testing, results were also highly congruent when analysing sites individually (Figs. S2, S3 and S4, Tables S8, S9 and S10).

3.4. Temporal overlap versus spatial co-occurrence

Estimates of temporal overlap (\widehat{O}_{est}) were correlated with the frequency with which species pairs are observed in the same photograph (spatial co-occurrence; see Tables S11 and S12). However, the strength of the correlation between the estimated temporal overlap coefficient and observed spatial co-occurrence varied between years (Spearman correlation = 0.43 and 0.27 for 2015 and 2022, respectively), with the correlation in 2022 largely driven by a few observations, with zebra and hyena having high leverage (Fig. S5).

4. Discussion

Many parks in Africa, including the world-famous Kruger National

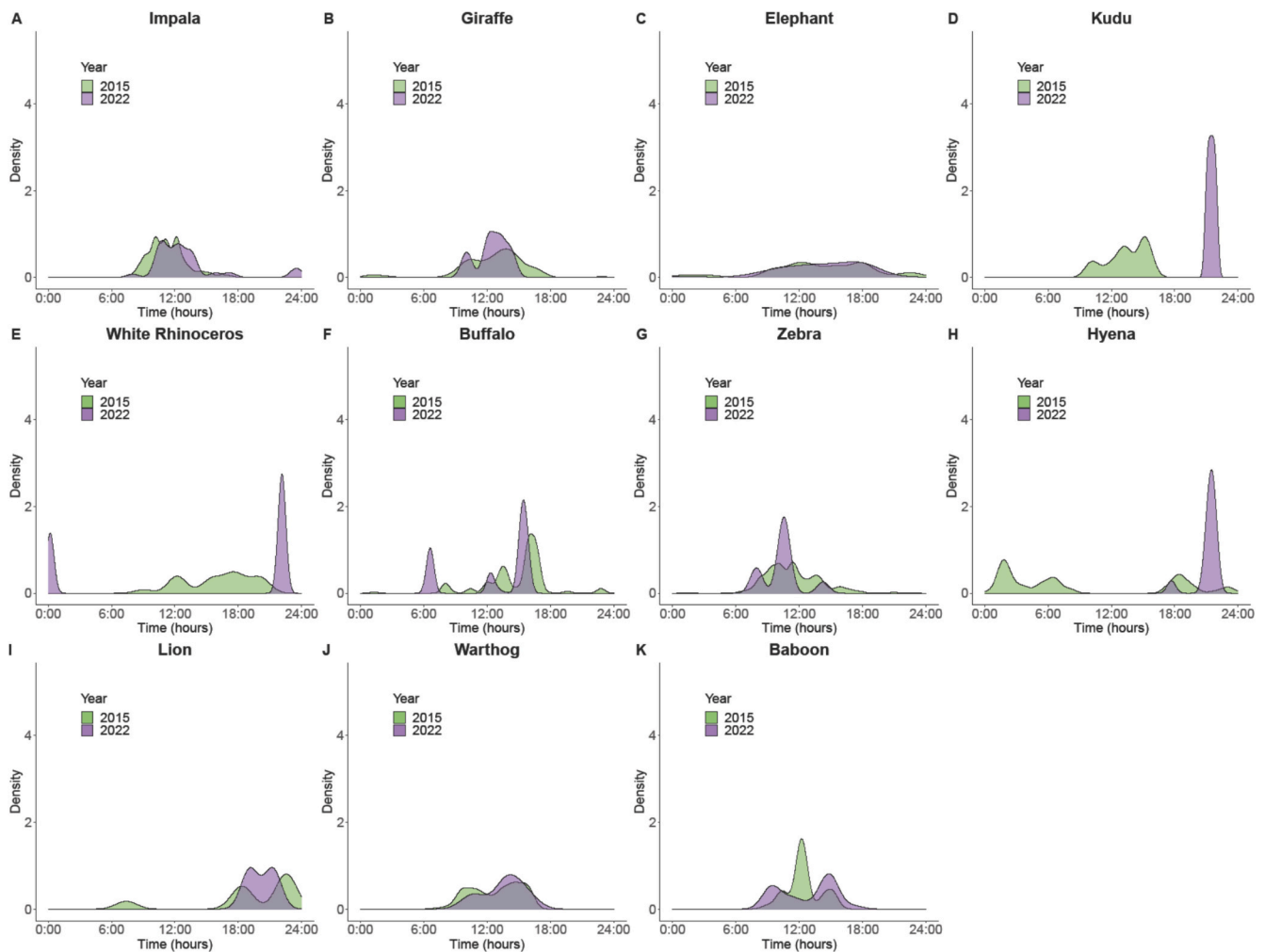


Fig. 3. Temporal overlap in activity patterns between years. Estimated temporal coefficient of overlap, (\widehat{O}_{est}), for each species (A–K) between 2015 and 2022. Green represents 2015 temporal visitation patterns and purple represents 2022 temporal visitation patterns, shaded grey area indicates overlap between years. The y-axis shows the density of the species visitations and the x-axis shows time over a 24-hour period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Park, have introduced artificial waterholes to support water-dependent species (Pienaar et al., 1997). However, the introduction of permanent water points has shifted ecological dynamics, favouring water-limited species and altering species interactions (Smit et al., 2007; Perkins, 2020; Smit et al., 2020). The impact of such artificial waterholes on wildlife is likely to be magnified with climate change. Because there happened to be collected camera trap data from an eDNA study during the 2015–2016 drought (Farrell et al., 2022), we had a unique opportunity to examine the impact of this extreme climate event on species' waterhole visitation patterns by comparing observations with data from a year with above average rainfall.

We show that many species display large differences in artificial waterhole visitation patterns between the drought and non-drought years which results in both increases and decreases in temporal overlap between species. There are competing hypothesis as to how species might adjust waterhole visitation patterns in drought years, shifting earlier in the day to avoid peak temperatures, or shifting to hotter parts of the day if access to water provides a relief from heat (Ayeni, 1975) or to reduce predation risk (Valeix et al., 2009a, 2009b; Hayward and Hayward, 2012). We find some evidence in support of both strategies, with different species exhibiting different responses, likely reflecting species' physiological water dependencies and vulnerability to predation (Valeix et al., 2009a, 2009b; Valeix, 2011). One consequence of these idiosyncratic responses is a shift in interspecific interactions as, for

example, some species that would normally partition waterhole use to avoid competition may now come into contact more frequently, while other species interactions may become rarer. Our results highlight the complexity in predicting how ecological dynamics might shift during periods of drought and unusual weather, with species adjusting both their spatial and temporal behaviours.

In the savanna ecosystem, species can be broadly classified according to their water dependency. For example, Hayward and Hayward (2012) classified hippopotamus, warthog and wildebeest as highly water-dependent, and lion, spotted hyena and kudu as water-independent. Generally, grazers, including impala and zebra, are considered to be more water-dependent than browsers (Western, 1975). Water-dependent species typically stay within the near vicinity (~15 km) of a water source, while water-independent species can go days without drinking and may travel long distances from water (Kihwele et al., 2020). In drought years, we might expect water-independent species to alter their waterhole visitation patterns more than water-dependent species, locating themselves nearer water sources and visiting more frequently in drier years. Supporting predictions, we observed large shifts in waterhole visitation patterns between the drought versus non-drought years for hyena, kudu and white rhinoceros (a grazer), while visitation patterns for impala and warthog were virtually unchanged. Lions were an exception to these general trends as they did not alter their waterhole visitation patterns as dramatically as other water independent

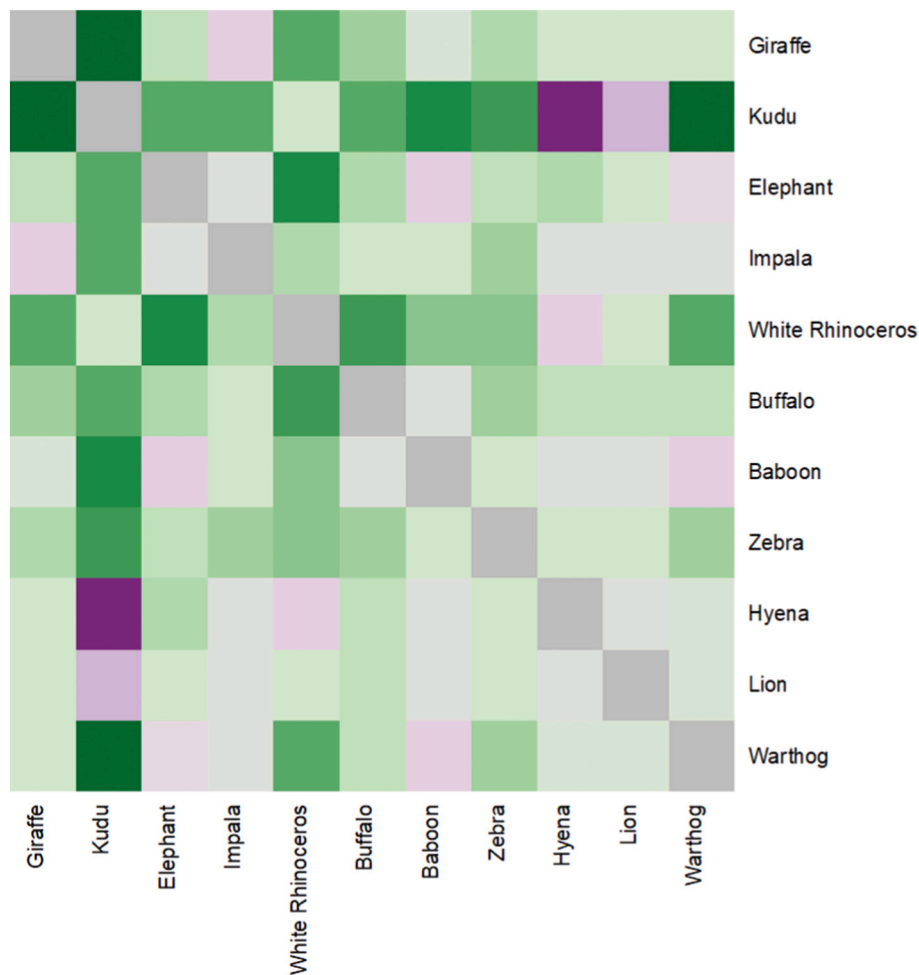


Fig. 4. Heatmap showing difference in temporal overlap among species pairs between 2015 and 2022 ($\Delta \widehat{O}_{est}$). Negative values (purple shading) indicate a larger overlap between species pairs in 2022 vs 2015. Positive values (green shading) indicate a larger overlap between species pairs in 2015 vs 2022. Intensity of shading reflects magnitude of change in overlap. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

species; it is possible that access to prey was more critical than water availability for this large predator.

We looked for changes in species’ potential for interaction by examining differences in temporal overlap between species pairs. We found evidence for both increases and decreases in temporal overlap, for instance, we document increasing temporal overlap between kudu and giraffe but greater temporal displacement between kudu and hyena. However, shifts to greater temporal overlap in the drought year dominate, such as shown between giraffe and kudu. In this species pair, giraffes do not depart from the null expectation of no difference between years, but kudu show a highly significant shift in daily waterhole visitation patterns from largely nocturnal visits during the non-drought year to visiting waterholes in the early afternoon during the drought year. Therefore, the greater temporal overlap between giraffe and kudu in the drought year appears to be largely driven by kudu aligning their waterhole visitation patterns with giraffe by shifting visits to earlier in the day. In non-drought years these two species tend to overlap less, perhaps to avoid competition, whereas in drought years kudu may benefit from interspecific aggregation in risky areas, such as open waterhole sites, to reduce predation risk via dilution (see [Hayward and Hayward, 2012](#)). [Moll et al. \(2016\)](#) suggest aggregation is one of the most common anti-predator strategies in ungulates. However, our data do not allow a direct test of the dilution or increased vigilance hypotheses as we lack contemporaneous data on predator proximity and predation rates.

We also observed greater temporal overlap between giraffe and lion

in the drought year ($\widehat{O}_{est} = 0.0$ and 0.13 in the non-drought and drought year respectively), although informed by few observations of lion. This species pair represents a potential predator-prey interaction, which we would assume giraffe would prefer to minimise. Lower temporal overlap in the non-drought year could translate to reduced mortality rates by predation in wetter years (see e.g. [Funston and Mills, 2006](#)). As a corollary, greater temporal overlap in drought years might suggest that giraffe may be experiencing water stress such that they visit waterholes even when predation risk is elevated (see also [Amoroso et al., 2020](#)). Impala, another prey species, shifted waterhole visitation patterns to be more concentrated earlier in the day in the drought year. This behavioural change is consistent with hypotheses associated with avoidance of higher temperatures later in the day and reduction in predation risk from lion ([Valeix et al., 2009a, 2009b](#); [Kasiringua et al., 2017](#)), which we show peak in waterhole visitation in the late afternoon.

In addition to reshaping species direct ecological interactions, we also suggest that increased temporal overlap of several large herbivore species pairs in the drought year, including kudu and giraffe, buffalo and impala, and buffalo and white rhinoceros, may have significant consequences for wildlife disease dynamics within the park. For example, buffalo and kudu are reservoir hosts for bovine TB, and changes in their potential interspecific interaction strengths could alter TB spillover risk. Notably, the first reported case of bovine TB in rhinoceros within the Kruger Park was documented immediately following the 2015 drought ([Dwyer et al., 2022](#)). While we are unable to directly explore disease transmission from camera trap data, shifting multi-host disease

dynamics is an important area in need of further study and it is possible to use observational data on species co-occurrence to inform transmission parameters in wildlife disease models (e.g. Barroso et al., 2023).

4.1. Temporal overlap versus co-occurrence

The daily waterhole visitation patterns we report are derived from photographs taken over a period of weeks across multiple waterholes, thus the analysis of temporal overlap we present here might not necessarily reflect species realised interactions. We therefore conducted two additional supporting analyses. First, we explored temporal overlaps at a finer grain, and separately examined changes between years at individual sites sampled across years. Consistent with observations aggregated across sites, we again found higher temporal overlap between elephant and buffalo, and buffalo and white rhinoceros in drought years. We do detect some notable differences in individual species behaviour when aggregated across sites versus site specific observations. For example, elephants do not show significant changes in temporal overlap between drought and non-drought years when all sites are analysed together, but we detect a significant shift in waterhole visitation patterns locally. Elephants might thus maintain relatively constant waterhole visitation patterns, but water scarcity may alter their space use. Second, we tested whether species with larger estimated temporal overlaps were seen together more frequently in the same photographs from camera traps by examining the correlation between estimated temporal overlaps and the frequency with which species pairs were observed together. In the drought year, for which we had a much larger sample of photographs, we found a medium to high correlation, indicating that temporal overlap provides a reasonable proxy for co-occurrence.

4.2. Management implications

Our study provides evidence that species may shift their visitation patterns at artificial waterholes during drought, changing species interaction frequencies with cascading ecological consequences. The establishment of artificial water points is a key management tool to address warming temperatures and increasing frequency of droughts in arid systems (Weeber et al., 2020). However, a growing body of evidence has highlighted negative impacts of artificial waterholes (see review by Perkins, 2020), and since the mid-1990s the KNP has removed around two-thirds of borehole fed waterholes (Smit et al., 2020). The decision whether to maintain or remove the remaining artificial waterholes thus presents a management dilemma.

We have shown that, in a drought year, species' visitation patterns at waterholes differed significantly in both frequency of visitation and, perhaps more critically, time of day. This has significant implications with respect to (1) intensity of direct ecological interactions between herbivores, which might compete for increasingly limited forage, (2) predator-prey dynamics, as prey species expose themselves to greater risk from predation when water is scarce, and (3) interspecific disease transmission. We suggest that these may represent additional ecological costs associated with artificial water points during extreme weather events, such as drought. As the climate continues to warm these effects will likely be further magnified. However, long-term studies on population and community dynamics are needed to determine whether costs outweigh benefits. Because of non-stationarity in climate, simply removing artificial waterholes will no longer return the ecosystem to its 'natural state' prior to their introduction.

Statement on inclusion

The data included in this study were collected in consultation with, and with feedback from, stakeholders at South African National Parks (SANParks). We include Danny Govender (GM, Sustainable Development and Management, SANParks) as co-author in recognition of this invaluable contribution to the research project design and execution.

CRediT authorship contribution statement

Ngaatendwe Ndachena: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Marjolein E.M. Toorians:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Maxwell J. Farrell:** Writing – review & editing, Methodology, Data curation. **Danny Govender:** Writing – review & editing, Data curation. **T. Jonathan Davies:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors have no conflict of interest to declare. D. Govender is an employee of SANParks.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111370>.

Data availability

The data that supports the findings of this study are available at <https://doi.org/10.5063/F1ZS2TZ9>.

References

- Amoroso, C.R., Kappeler, P.M., Fichtel, C., Nunn, C.L., 2020. Temporal patterns of waterhole use as a predator avoidance strategy. *J. Mammal.* 101 (2), 574–581. <https://doi.org/10.1093/jmammal/gyaa020>.
- Ayeni, J.S.O., 1975. Utilization of waterholes in Tsavo National Park (east). *Afr. J. Ecol.* 13 (3–4), 305–323.
- Barroso, P., Relimpio, D., Zearra, J.A., Cerón, J.J., Palencia, P., Cardoso, B., Ferreras, E., Escobar, M., Caceres, G., López-Olvera, J.R., Gortázar, C., 2023. Using integrated wildlife monitoring to prevent future pandemics through one health approach. *One Health* 16, 00479.
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Martínez-Santalla, S., Martín-Devesa, R., Gomez-Rodríguez, C., Crujeiras, R., 2023. Betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.6. <https://CRAN.R-project.org/package=betapart>.
- Bates, A.E., Primack, R.B., Biggar, B.S., Bird, T.J., Clinton, M.E., Command, R.J., Richards, C., Shellard, M., Gerald, N.R., Vergara, V., Acevedo-Charry, O., 2021. Global COVID-19 lockdown highlights humans as both threats and custodians of the environment. *Biol. Conserv.* 263, 109175.
- Craigie, I.D., Baillie, J., Balmford, A., Carbone, C., Collen, B., Green, R.E., Hutton, J., 2010. Large mammal population declines in Africa's protected areas. *Biol. Conserv.* 143 (9), 2221–2228. <https://doi.org/10.1016/j.biocon.2010.06.007>.
- Davies, T.J., Daru, B.H., Bezeng, B.S., Charles-Dominique, T., Hempson, P.G., Kabongo, M.R., Maurin, O., Muasya, M.A., Van der Bank, M., Bond, J.W., 2020. Savanna tree evolutionary ages inform the reconstruction of the paleoenvironment of our hominin ancestors. *Sci. Rep.* 10, 12430. <https://doi.org/10.1038/s41598-020-69378-0>.
- Di Marco, M., Buchanan, G.M., Szantoi, Z., Holmgren, M., Marasini, G.G., Gross, D., Tranquilli, S., Boitani, L., Rondinini, C., 2014. Drivers of extinction risk in African mammals: the interplay of distribution state, human pressure, conservation response and species biology. *Philos. Trans. R. Soc. B* 369 (1643), 20130198. <https://doi.org/10.1098/rstb.2013.0198>.
- Dwyer, R., Goosen, W., Buss, P., Kedward, S., Manamela, T., Hausler, G., Chileshe, J., Rossouw, L., Fowler, J.H., Miller, M., Witte, C., 2022. Epidemiology of *Mycobacterium bovis* infection in free-ranging rhinoceros in Kruger National Park, South Africa. *Proc. Natl. Acad. Sci.* 119 (24), e2120656119.
- Engelbrecht, F., Adegoke, J., Bopape, M.J., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., Werner, M., Ichoku, C., Gatebe, C., 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environ. Res. Lett.* 10 (8), 085004. <https://doi.org/10.1088/1748-9326/10/8/085004>.
- Farrell, M.J., Govender, D., Hajibabaei, M., Van Der Bank, M., Davies, T.J., 2022. Environmental DNA as a management tool for tracking artificial waterhole use in savanna ecosystems. *Biol. Conserv.* 274, 109712. <https://doi.org/10.1016/j.biocon.2022.109712>.
- Funston, P.J., Mills, M.L.G., 2006. The influence of lion predation on the population dynamics of common large ungulates in Kruger National Park: research article. *S. Afr. J. Wildl. Res.* 36 (1), 9–22. Available from: <https://journals.co.za/doi/epdf/10.10520/EJC117232>.
- Hayward, M., Hayward, M.D., 2012. Waterhole use by African fauna. *S. Afr. J. Wildl. Res.* 42 (2), 117–127. <https://doi.org/10.3957/056.042.0209>.

- Janis, C.M., Damuth, J., Theodor, J.M., 2000. Miocene ungulates and terrestrial primary productivity: where have all the browsers gone? *Proc. Natl. Acad. Sci. U. S. A.* 97 (14), 7899–7904. <https://doi.org/10.1073/pnas.97.14.7899>.
- Kasiringua, E., Kopij, G., Procheş, Ş., 2017. Daily activity patterns of ungulates at water holes during the dry season in the Waterberg National Park, Namibia. *Russian Journal of Theriology* 16, 129–138. <https://doi.org/10.15298/rusjtheriol.16.2.02>.
- Kihwele, E.S., Mchomvu, V., Owen-Smith, N., Hetem, R.S., Hutchinson, M.C., Potter, A. B., Olf, H., Veldhuis, M.P., 2020. Quantifying water requirements of African ungulates through a combination of functional traits. *Ecological monographs* 90 (2). <https://doi.org/10.1002/ecm.1404>.
- Malherbe, J., Dieppois, B., Maluleke, P., et al., 2016. South African droughts and decadal variability. *Nat. Hazards* 80, 657–681. <https://doi.org/10.1007/s11069-015-1989-y>.
- Malherbe, J., Smit, I.P., Wessels, K.J., Beukes, P.J., 2020. Recent droughts in the Kruger National Park as reflected in the extreme climate index. *African Journal of Range & Forage Science* 37 (1), 1–17. <https://doi.org/10.2989/10220119.2020.1718755>.
- Maurin, O., Davies, T.J., Burrows, J.E., Daru, B.H., Yessoufou, K., Muasya, A.M., Van Der Bank, M., Bond, W.J., 2014. Savanna fire and the origins of the ‘underground forests’ of Africa. *New Phytol.* 204 (1), 201–214. <https://doi.org/10.1111/nph.12936>.
- Moll, R.J., Killion, A.K., Montgomery, R.A., Tambling, C.J., Hayward, M.W., 2016. Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology* 97 (5), 1123–1134. <http://www.jstor.org/stable/24703792>.
- Perkins, J.S., 2020. Changing the scale and nature of Artificial Water Points (AWP) use and adapting to climate change in the Kalahari of Southern Africa. In: Keitumetse, S. O., Hens, L., Norris, D. (Eds.), *Sustainability in Developing Countries: Case Studies from Botswana’s Journey towards 2030 Agenda*. Springer, Cham, pp. 51–89. https://doi.org/10.1007/978-3-030-48351-7_4.
- Pienaar, D.J., Biggs, H.C., Deacon, A., Gertenbach, W., Joubert, S., Nel, F., Venter, F., 1997. A revised water-distribution policy for biodiversity maintenance in the Kruger National Park. *Kruger Park Management Plan* 8, 165–200. Retrieved from <https://africawild-forum.com/download/file.php?id=15298>.
- Ramankutty, N., Foley, J.A., 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochem. Cycles* 13 (4), 997–1027. <https://doi.org/10.1029/1999gb900046>.
- Ridout, M., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* 14 (3), 322–337. <https://doi.org/10.1198/jabes.2009.08038>.
- Roux, D.J., Foxcroft, L.C., 2011. The development and application of strategic adaptive management within South African National Parks. *Koedoe* 53 (2), 1–5. <https://hdl.handle.net/10520/EJC132247>.
- Smit, I.P., Grant, C., Devereux, B., 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biol. Conserv.* 136 (1), 85–99. <https://doi.org/10.1016/j.biocon.2006.11.009>.
- Smit, I.P., Peel, M., Ferreira, S.M., Greaver, C., Pienaar, D., 2020. Megaherbivore response to droughts under different management regimes: lessons from a large African savanna. *Afr. J. Range Forage Sci.* 37 (1), 65–80. <https://doi.org/10.2989/10220119.2019.1700161>.
- Thrash, I., Theron, G., Du P Bothma, J., 1995. Dry season herbivore densities around drinking troughs in the Kruger National Park. *J. Arid Environ.* 29 (2), 213–219. [https://doi.org/10.1016/s0140-1963\(05\)80091-6](https://doi.org/10.1016/s0140-1963(05)80091-6).
- Titcomb, G., Mantas, J.N., Hulke, J., Rodriguez, I., Branch, D., Young, H., 2021. Water sources aggregate parasites with increasing effects in more arid conditions. *Nat. Commun.* 12 (1), 7066.
- Valeix, M., 2011. Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe. *J. Trop. Ecol.* 27 (2), 163–170.
- Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J., Murindagomo, F., Macdonald, D.W., 2009a. Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioural Ecology and Sociobiology* 63 (10), 1483–1494. <https://doi.org/10.1007/s00265-009-0760-3>.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., Macdonald, D.W., 2009b. Behavioural adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90 (1), 23–30. <http://www.jstor.org/stable/27650944>.
- Van Wyk, L., 2001. Review of the ecological implications of artificial waterhole closures in the Kruger National Park and the effect thereof on tourism. ProQuest Dissertations Publishing, 28288549. Retrieved from <https://www.proquest.com/docview/2531159393?pq-origsite=gscholar&fromopenview=true>.
- Walker, B.H., Emslie, R.H., Owen-Smith, R.N., Scholes, R.J., 1987. To cull or not to cull: lessons from a southern African drought. *J. Appl. Ecol.* 24 (2), 381–401. <https://doi.org/10.2307/2403882>.
- Wato, Y.A., Heitkonig, I., Van Wieren, S.E., Wahungu, G., Prins, H.H.T., Van Langevelde, F., 2016. Prolonged drought results in starvation of African elephant (*Loxodonta africana*). *Biol. Conserv.* 203, 89–96. <https://doi.org/10.1016/j.biocon.2016.09.007>.
- Weeber, J., Hempson, G.P., February, E.C., 2020. Large herbivore conservation in a changing world: surface water provision and adaptability allow wildebeest to persist after collapse of long-range movements. *Glob. Chang. Biol.* 26 (5), 2841–2853. <https://doi.org/10.1111/gcb.15044>.
- Western, D., 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *Afr. J. Ecol.* 13, 265–286. <https://doi.org/10.1111/j.1365-2028.1975.tb00139.x>.
- Zambatis, N., Biggs, H., 1995. Rainfall and temperatures during the 1991/92 drought in the Kruger National Park. *Koedoe* 38 (1). <https://doi.org/10.4102/koedoe.v38i1.301>.