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Heterogeneity of water physico-chemical characteristics in artificially pumped waterholes: do African herbivores drink at the same locations and does it lead to interference competition?

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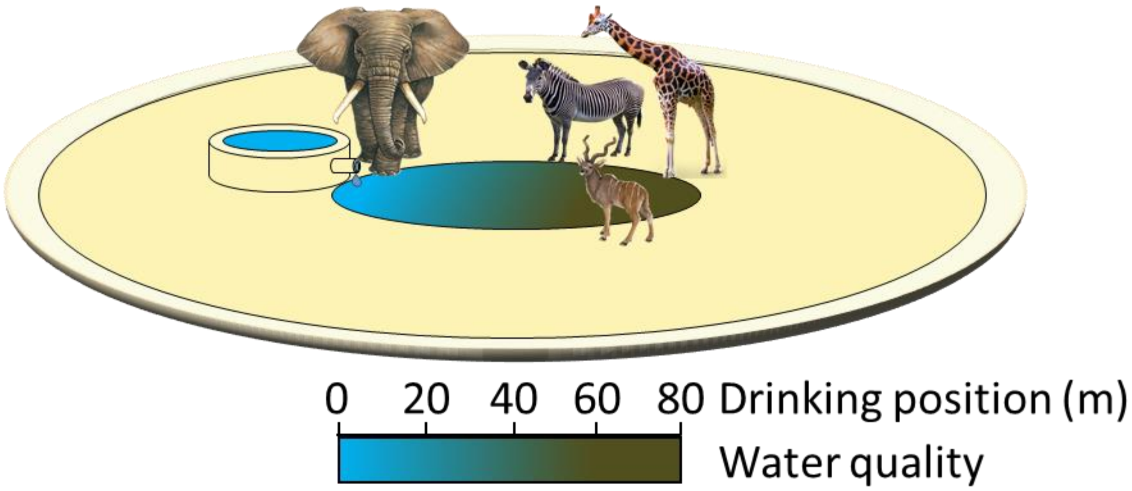
Abstract

In many semi-arid savanna ecosystems, surface water is scarce and only found in artificially pumped waterholes at the end of the dry season, leading to high large mammal densities and competition. Further, the modification of the physico-chemical characteristics of the drinking water over the dry season (e.g. through faeces accumulation) could enhance competition. Indeed, elephants, considered as key-competitor, and other herbivores by aggregating near the trough where clear water arrives could compete for this resource. We studied the drinking locations of eight herbivore species around pumped waterholes in relation to these water characteristics in Hwange National Park, Zimbabwe. We identified differences of the physico-chemical characteristics of the water in different sections of pumped waterholes at the end of the dry season. Elephants drank the water in or close to the trough, whereas other species drank further in the waterhole, except roan and sable antelopes which were indifferent about where they drank. Interference competition with elephants for the access to water close to the trough was not detected for zebras and kudus. We discuss possible directions for future research to enhance our understanding of waterhole use by herbivores.

Graphical abstract



Highlights

1. Water physico-chemical characteristics (e.g. total organic content, nitrate, turbidity and temperature) are heterogeneous inside artificially pumped waterholes, depending on the distance to the trough.
2. African elephants drink closer to the trough than other species, sable and roan antelopes do not show any specific pattern and have a high variability in their drinking position, and other herbivore species drink far from the trough.
3. Studied species do not drink at the same time as elephants, except kudus and zebras.
4. Kudus and zebras do not drink closer to the trough when elephants are absent, showing an absence of interference competition for the cleaner water close to the trough.

Keywords

Interference competition, large African herbivores, resource quality heterogeneity, spatial aggregation, semi-arid savanna, waterhole scale**.**

1. Introduction

Species distribution patterns depend on the spatial distribution of resources (O'neill *et al.* 1988, Pearson 1993). Patches of resources represent attractive areas in the landscape, around which animals are likely to aggregate and may temporarily form mixed-species groups (Waser 1982, Stendland *et al.* 2003). The co-occurrence of different species can lead to interspecific competition (exploitative or interference, Schoener 1983), forcing some species to avoid more competitive ones at both spatial (Durant 2000, Tannerfeldt *et al.* 2002) and temporal scales (Ziv *et al.* 1993, Valeix *et al.* 2007). The intensity of these competition processes increases as resource quantity or accessibility decreases. This is typically the case of surface water resources in arid and semi-arid ecosystems, where water resources dry up as the dry season progresses. In many arid and semi-arid savanna ecosystems, surface water during the dry season is provided mainly through artificial pumping of underground water. These pumped waterholes often represent the only source of surface water available to animals at the end of the dry season. This scarcity of water leads to the aggregation of a wide range of large mammal species around pumped waterholes, sometimes at very high levels of abundance (Weir & Davison 1965, Valeix 2011).

While several studies have focused on the use of pumped waterholes by large wild mammal species (Western 1975, Redfern *et al.* 2003, Hayward & Hayward 2012), our understanding of the underlying processes of co-occurrence patterns of different species is still incomplete. Interspecific competition is likely to be a major process taking place between species simultaneously exploiting water resources. For example, Valeix *et al.* (2007) showed a temporal avoidance of African elephants *Loxodonta africana* by several other herbivores species. However, a recent study revealed that when zebras *Equus quagga*, and to a lesser extent kudus *Tragelaphus strepsiceros*, co-occur with elephants around pumped waterholes at the end of the dry season, they tend to all aggregate in the same specific sections of the waterhole area

(Ferry *et al.* 2016). One hypothesis suggested to explain this unexpected result is that it is not only the presence or the quantity of the resource that matters but its quality. Here, we thus focused on the physico-chemical characteristics of water. The documented patterns of species positions around pumped waterholes may result from a passive aggregation with species being attracted by the same characteristics of the water (e.g. sufficient level of some mineral nutrients, low organic matter content) in particular areas of the waterholes. Numerous studies have reported that animals select patches with food of higher quality (e.g., Langvatn & Hanley 1993; Wilmshurst *et al.*1995, Van der Wal *et al.* 2000, Hochman & Kotler 2006). However, studies on the influence of the quality of water resources on wild animals drinking behaviour are rare (but see Wanke & Wanke 2006, Chamaillé-Jammes *et al.* 2007). At a fine scale, nothing is really known about the role of the spatial heterogeneity of water characteristics in waterholes on drinking choices and surface water use.

Herbivores are active carriers of nutrients when they urinate and defecate in water (Naiman & Rogers, 1997, Masese *et al.* 2015, Subalusky *et al.* 2015, Hulot *et al. unpublished data*). It is therefore possible that the combined effect of evaporation and accumulation of herbivore faeces and urine in waterholes as the dry season progresses leads to a change in the physico-chemical characteristics of the water in most waterholes (e.g. Gereta & Wolanski 1998, Strauch 2013, Msiteli-Shumba *et al. 2018*) and to a spatial gradient of these characteristics in pumped waterholes. In these artificially pumped waterholes, the presence of an area where the clear pumped water arrives could lead herbivores to actively seek for this water with specific physico-chemical characteristics (Wanke & Wanke 2006). Under this water gradient hypothesis, elephants and most other herbivores are expected to end up being aggregated as the dry season progresses just because the water coming from the trough, which represents the area where fresh water arrives in the waterhole, attracts them all.

Here, we studied the physico-chemical characteristics of the water in different areas of pumped waterholes in the semi-arid savanna of Hwange National Park, Zimbabwe, where we also monitored the positioning of different herbivore species when they drink at these waterholes. We tested the hypothesis that the heterogeneity of water physico-chemical characteristics in a waterhole explains aggregation patterns at attractive areas of the waterhole, and ultimately may lead to interference competition between elephants and other herbivore species. We predicted (i) the existence of a gradient of water physico-chemical characteristics at the waterhole scale at the end of the dry season, (ii) the attraction of troughs where pumped underground water emerges, represented by a low distance between drinking herbivores and the trough, and (iii) an interference competition between elephants (the largest and a potentially aggressive species – Valeix *et al.* 2007) and other herbivore species for the access to water of better physico-chemical properties, resulting in a higher distance to the trough when drinking in the presence of elephants compared to situations without elephant.

2. Materials and methods

2.1 Study site

The study area (~7 000km²) is located in the northern region of Hwange National Park which covers ~15 000 km² of semi-arid dystrophic (low nutrient soil) savanna in north-western Zimbabwe (19°00' S, 26°30' E; Fig. 1). The vegetation is primarily woodland and bushland savanna. The long-term mean annual rainfall is ~ 600 mm, which falls primarily between November and April, and the dry season stretches from May to October. The surface water available to animals is found in natural waterholes and rivers as well as artificially pumped waterholes. Waterholes are depressions that are fed by rainwater during the rainy season. During the dry season, many waterholes are supplied with pumped underground water. Water is extracted from boreholes using solar panel-powered pumps (so water is extracted during the day). Water is first pumped into an open-top concrete ground-level small drinking trough, and then flows continually from the trough to the depression (see Appendix 1 for pictures). Natural water bodies dry up during the dry season and only artificially pumped waterholes offer drinking water throughout the year and at the end of the dry season. In pumped waterholes, the pumping is continuous during the day when most herbivore species come to drink (Valeix et al. 2007) and the waterhole is then continually fed with pumped water. Eight herbivore species were monitored: two browsers (giraffe *Giraffa camelopardalis* and greater kudu), two mixed-feeders (African elephant and impala *Aepyceros melampus*) two woodland grazers (roan antelope *Hippotragus equinus*, and sable antelope *Hippotragus niger*) and two grassland grazers (warthog *Phacochoerus africanus* and Burchell's zebra).

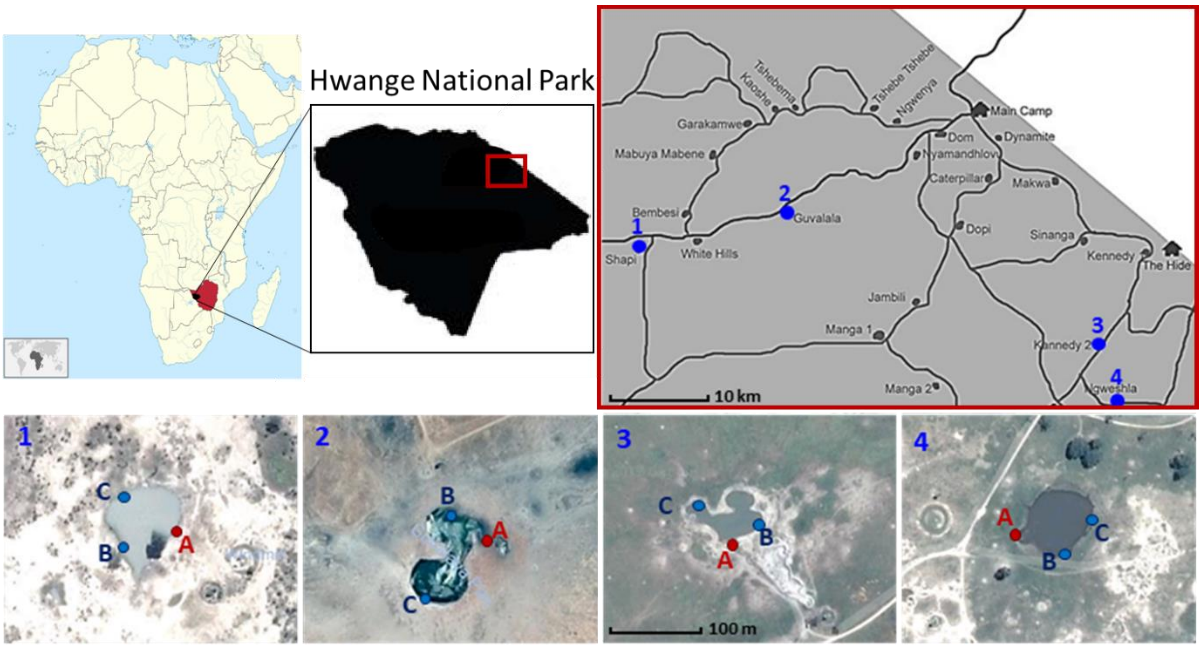


Figure 1: Map of the four monitored pumped waterholes in Hwange National Park, Zimbabwe. Locations of B and C (in blue, corresponding respectively to locations at intermediate and the longest distance from the trough) and A (in red, corresponding to the trough) for each waterhole. Aerial photos of the waterholes were taken from Google Map and scale bar is the same for all four waterholes.

2.2 Data

2.2.1 Water physico-chemical characteristics

We sampled the physico-chemical characteristics of the water in four monitored pumped waterholes (Fig. 1) in October 2017, i.e. at the end of the dry season. A water sample was collected in three different areas for each waterhole. The first sample was taken in the water near the trough (A), the second at the furthest location from the trough (C), and the third at an intermediate distance (B) (Fig. 1). For the four waterholes, the mean distance between A and C is 73.2 m (ranging from 61m at Shapi to 87 m at Guvalala) and represents the maximal distance to the trough when animals were drinking. Water samples were taken before 12 p.m. to minimize variability in the time of the day. We measured near the shoreline temperature, dissolved oxygen concentration, pH, turbidity and chlorophyll a concentration with a YSI 6600 VZ Multiparameter water probe. Conductivity was measured with a Hanna HI 98312 portable conductivity meter. Water conductivity measures the concentration in ions dissolved in water (calcium, magnesium, sodium, potassium, chloride, sulphate, nitrate and bicarbonate for the major ions). Water samples for laboratory analyses were collected on site at the deepest point with a bottle fastened to a 3 m pole. Water was stored on ice in one-litre polyethene bottles and was filtered back to the laboratory with GF/F 47 mm filters. Total nitrogen and total organic carbon concentrations and water hardness were determined from unfiltered water samples. Ammonium, nitrite, nitrate and orthophosphate concentrations were determined from filtered water samples. Chemical analyses were realized with a Hach DR 3900 portable data logging spectrophotometer and reagents in accordance with the manufacturer's procedure.

2.2.2 Drinking position

Observations of drinking herbivores were made at the same four monitored pumped waterholes (Fig. 1) between August and November 2016, i.e. at the end of the dry season. Every day, observations were done from 6 a.m. until 6 p.m at one of the study pumped waterholes. Observers were inside a car parked at approximatively 100m from the waterhole as a compromise between disturbance and quality of the observation. Each time an herbivore or a group of herbivores drank at the waterhole, the position of the closest individual to the trough (focal individual) was recorded. In order to calculate the distance between the drinking focal individual and the trough, we recorded the angle to the north (with a compass) and the distance from the car (with a range finder) of the focal individual and the trough. For all drinking observations of the herbivores, we recorded if elephants were present at the waterhole or not.

Drinking position and water physico-chemical characteristics were not studied the same year, but 2016 and 2017 were characterized by similar annual rainfall (438.3 and 477 mm respectively). Water availability depends on rainfall during the rainy season and evaporation and pumping during the dry season. Morphological characteristics (depth, shape) of the waterholes and trough position did not change between 2016 and 2017. We therefore assume that water had a comparable gradient of physico-chemical characteristics between these two years.

2.3 Analyses

Analyses were conducted using R v. 3.3 software (R Development Core Team, 2004).

2.3.1 Water physico-chemical characteristics

In order to assess the existence of a gradient of water physico-chemical characteristics inside waterholes, we performed multivariate analyses. First, a Principal Component Analysis (PCA, package ade4, Dray & Dufour 2007) was performed on the thirteen variables. We then removed the effect of the heterogeneity between waterholes with a within-class analysis and performed a between-class analysis to estimate the percentage of the remaining variability explained by the differences between the three locations A, B and C.

2.3.2 Drinking position

We first assessed the difference of position where animals drank at the waterhole between each study herbivore species by performing a mixed-model (package lmer, Bates 2008) on the distance to the trough when drinking. The species was considered as a fixed effect and the waterhole monitored as a random effect. A pairwise post-hoc comparison was then performed on the mixed-model between each pair of species (package lsmeans, Lenth 2016). The p-values were adjusted with the Tukey method. We then assessed the influence of elephant presence on the drinking position of other herbivore species. We performed a mixed-model with the distance to the trough when drinking as the dependant variable. The interaction between the presence of elephants when drinking and the herbivore species was introduced as an explanatory term in the fixed part of the model. This analysis could be carried out for kudus and zebras only as these two species were the only ones recorded both in the absence of elephants and with elephants at the study waterholes. The waterhole monitored was considered as a random effect.

3. Results

3.1 Water physico chemical characteristics

After the within-class analysis removed the variability due to differences between waterholes, the between-class analysis revealed that 31% of the remaining variability was explained by differences of water physico-chemical characteristics between the locations A, B and C. As the distance to the trough increases (from A to C), the concentration of total organic carbon, dissolved oxygen, total nitrogen and ammonium, and the conductivity increased whereas the temperature, the turbidity and the nitrate concentration decreased (Fig. 2, Fig. 3).

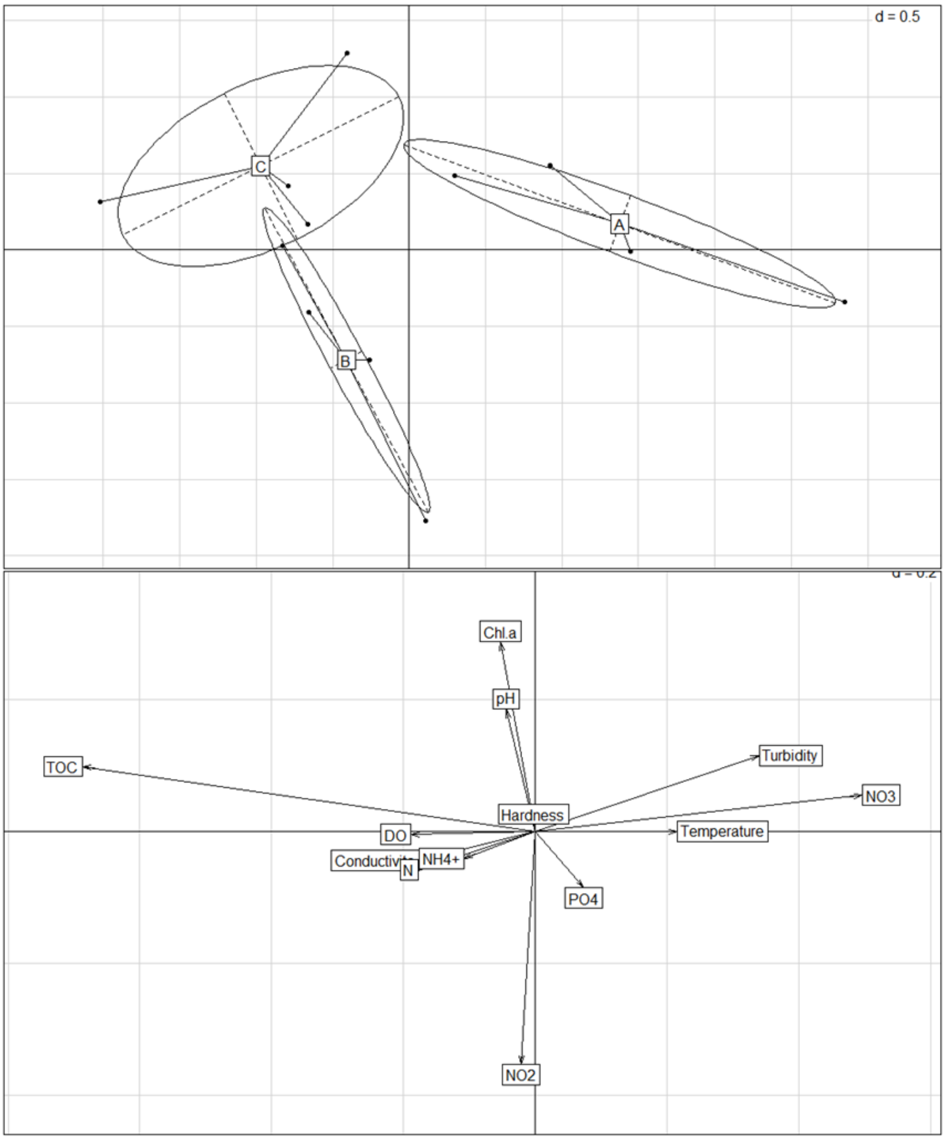


Figure 2: Graphical results of the between-class principal component analysis. Top: position of the four waterholes (black dots) with confidence ellipses around the categories defined by the distance to the trough (A, B and C). Bottom: position of the thirteen variables: dissolved oxygen (DO), total organic carbon (TOC), total nitrogen (N), ammonium (NH4+), nitrite (NO2), nitrate (NO3), orthophosphate (PO4) and chlorophyll a (Chl.a) concentration and conductivity (Conductivity), hardness (Hardness), turbidity (Turbidity) and temperature (Temperature).

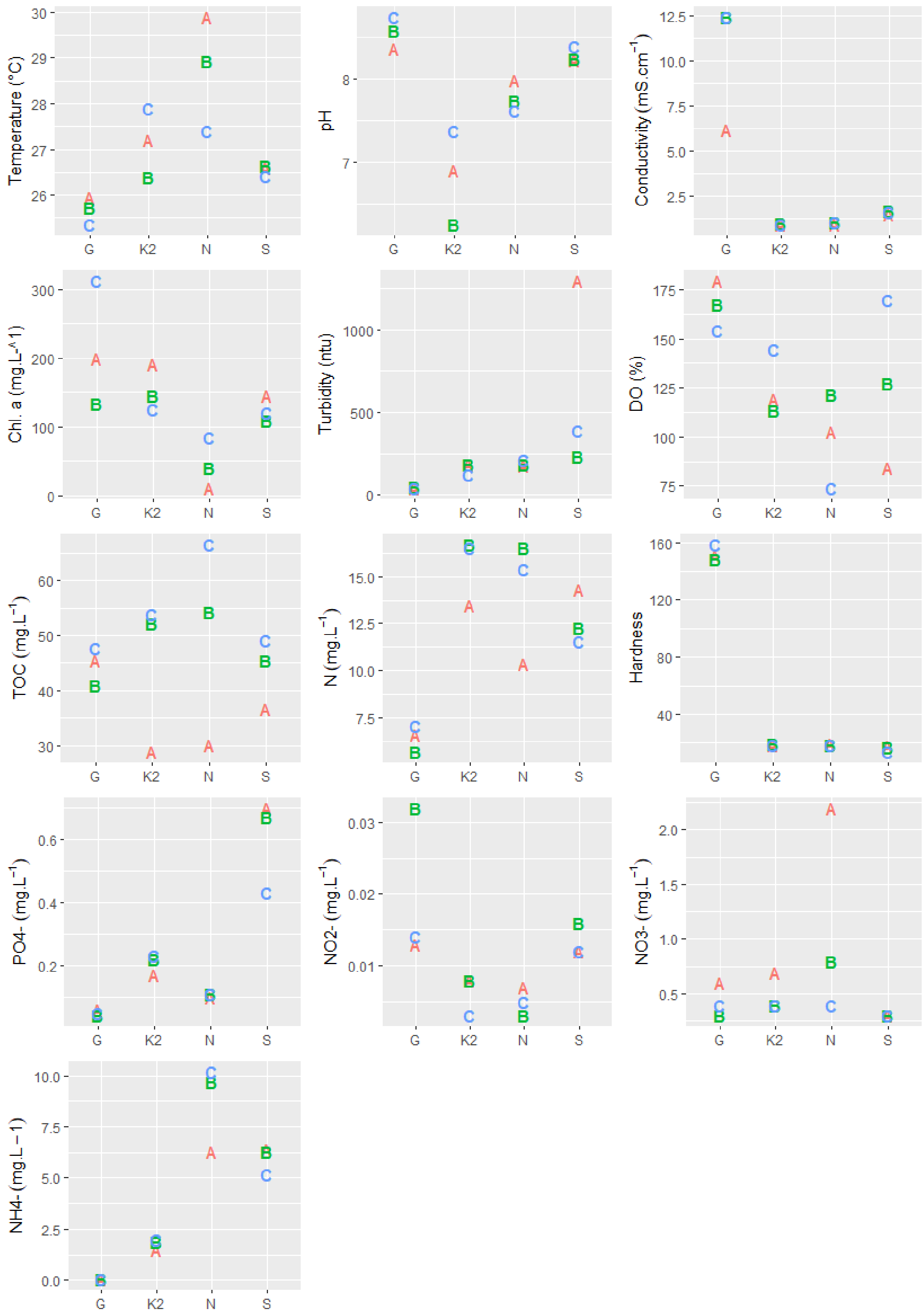


Figure 3: Physico-chemical characteristics of the three points (A, B and C) respectively close, intermediate and far from the trough in the four waterholes ("G" = Guvalala, "K2" = Kennedy

2, “N” = Ngweshla, “S” = Shapi). The thirteen studied physico-chemical characteristics are presented: dissolved oxygen (DO), total organic carbon (TOC), total nitrogen (N), ammonium (NH4+), nitrite (NO2), nitrate (NO3), orthophosphate (PO4) and chlorophyll a (Chl.a) concentration and conductivity (Conductivity), hardness (Hardness), turbidity (Turbidity) and temperature (Temperature). Regarding DWAF vol. 7 (1996) for aquatic ecosystem monitoring, the target water quality range is 7 mg.l^{-1} for ammonium (NH4+), between 80 and 120% for dissolved oxygen (DO) and the water is considered as hypertrophic if orthophosphate (PO4-) is above 0.25 mg.l^{-1}. Regarding DWAF vol. 1 (1996) on domestic water monitoring, if the chlorophyll a (Chl.a) is above 10 mg.l^{-1} the water “has a distinct murky appearance, becoming increasingly green in colour with significant taste and odour problems and secondary growth bacteria on the distribution system”, if the hardness is below 50 the water is considered as soft, if it is between 150 and 200 the water is considered as “moderately hard”. Finally, if the turbidity is above 10 the water carries an associated risk of disease due to infectious disease agents and chemicals adsorbed onto particulate matter.

3.2 Drinking position

The mixed model allowed estimating the mean (± SE) drinking distance to the trough for the eight study species, which ranged from 15.5 m to 58.5 m (Fig. 4). Post-hoc tests revealed three different groups: (i) elephants, which drank the closest to the trough, (ii) roan and sable antelopes with an intermediate estimated mean distance from the trough, and (iii) all other study herbivore species (zebras, kudus, impalas, giraffes and warthogs), which drank the furthest from the trough (Fig. 4). A high variability was observed between waterholes, especially for roan and sable antelopes, which were observed to drink at highly variable distances from the trough (Fig. 5). No effect of the presence of elephants on the drinking distance from the trough was observed neither for zebras (β ± SE = 0.77 ± 6.56, t = 0.118, p = 0.9), nor for kudus (β ± SE = -1.11 ± 8.23, t = -0.13, p = 0.9).

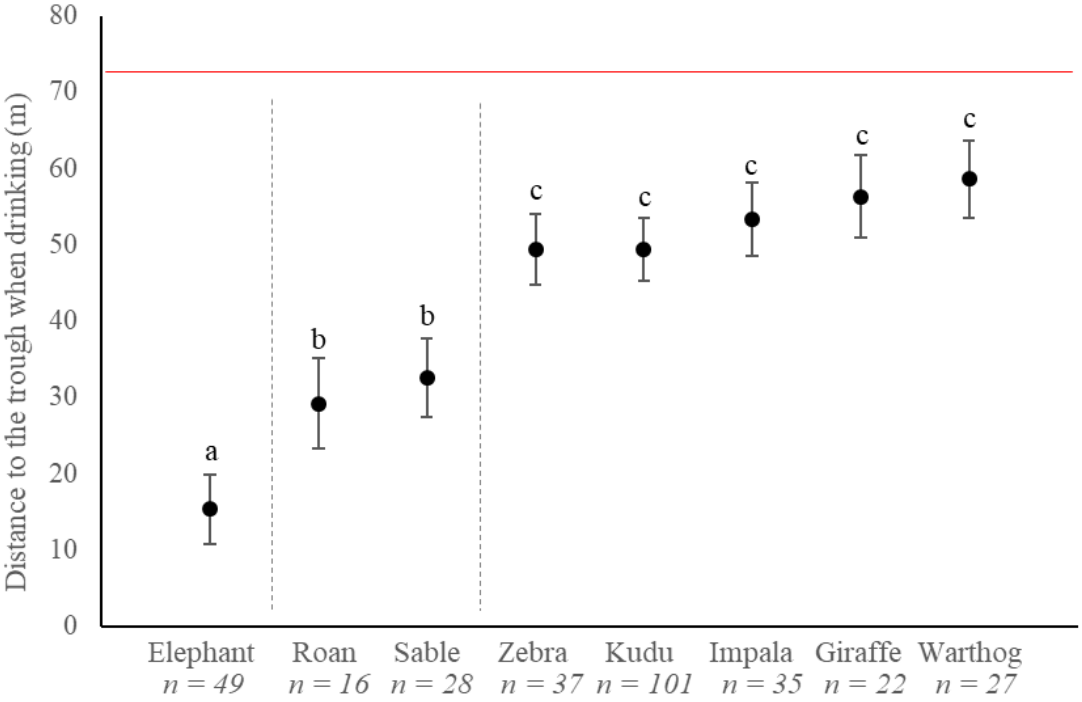


Figure 4: Estimated mean (± SE) of the distance to the trough for drinking individuals of the nine study herbivore species that visited the four study pumped waterholes in Hwange National Park, Zimbabwe. The number of observations (n) for each species is provided. Different letters

(a, b, c) indicate significant differences obtained by pairwise post-hoc comparison on the mixed-model between each pair of species. Red line indicates maximum distance averaged between the four waterholes.

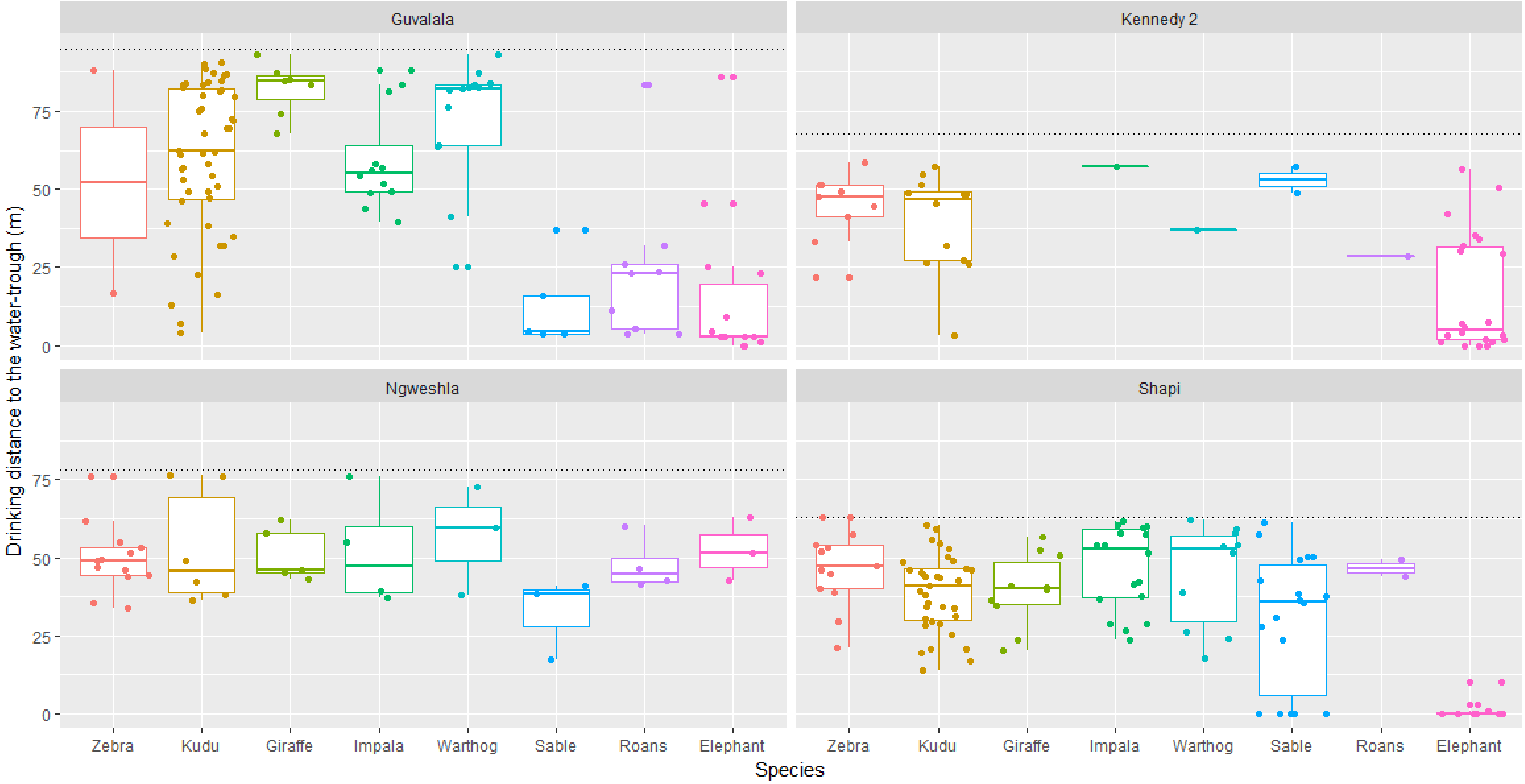


Figure 5: Distance to the trough for drinking individuals of the eight study herbivore species that visited the four study pumped waterholes in Hwange National Park, Zimbabwe. Dotted lines represent the maximum drinking distance at the time of the monitoring for each study waterhole.

4. Discussion

In this study, we identified differences of water physico-chemical characteristics at the scale of the waterhole at the end of the dry season. We then showed that elephants drank the water that flowed from the trough, that all other studied species drank relatively far from the trough except roan and sable antelopes, which were indifferent about where they drank. Finally, we did not detect any spatial patterns indicative of interference competition for the access to freshly pumped water between elephants and zebras or kudus.

4.1.Water physico-chemical characteristics

Our results revealed differences of water physico-chemical characteristics in different sections of pumped waterholes at the end of the dry season. Indeed, troughs are set up between the outlet of the pump and the waterhole and provide water of the same characteristics as the underground water to the animals because the trough is continually flushed (Wanke & Wanke, 2007). This water is generally less salty and conductive than surface water. Given that there is no input of rainwater in the dry season, evaporation and changes due to fauna activity lead to changes of the physico-chemical characteristics of the water in the waterhole (Wanke & Wanke 2007, Msiteli-Shumba *et al. 2018*), in particular with the concentration of ions which lead to an increase in conductivity and salinity.

Far from the trough, the water is enriched in organic matter (high concentration of total organic carbon, total nitrogen) and degradation product (ammonium). This organic matter may be inherent to the presence of microorganisms in the waterhole (Strauch 2013), but also to urine and faeces of the numerous animals drinking in the waterhole. This last source of contamination is indeed frequently mentioned in the literature (e.g. Gereta & Wolanski 1998, Strauch 2013, Hulot *et al. unpublished data*). These organic matter inputs may stimulate phytoplankton growth, leading to high concentrations of chlorophyll *a* and dissolved oxygen, and lead to the high turbidity and water eutrophication observed in Hwange National Park (Msiteli-Shumba *et al. 2018*) and can intensify heterogeneity of water characteristics between trough and the remaining waterhole. According to the criterions of the Department of Water and Sanitation in South Africa (DWAF, 1996), the water far from the trough is hypertrophic. No guideline exists for wildlife concerning water quality. However, the criterions for domestic water show that the high chlorophyll a concentration and turbidity are symptomatic of degraded water with significant taste and odour problems, secondary bacteria growth and risk of diseases due to infectious agents (DWAF 1996).

4.2. Drinking position

Several studies have documented how freshwater parameters influence terrestrial animals' drinking behaviour. For example, Auer (1997) showed that an increase of the water salinity led herbivores to sniff and taste the water extensively, try many positions at the waterhole, and sometimes leave the waterhole without drinking. Stommel *et al.* (2016) studied the response of some African mammals to total aerobic bacterial load and suggested that digging is an adaptation to avoid poor quality water and potentially pathogenic microbes. However, none focused on the heterogeneity at the scale of the waterhole.

Our results showed that elephants drank most of the time the water from the trough, except in Ngweshla (but only three observations observed at that waterhole). This confirms what Ramey *et al.* (2013) observed where elephants damaged borehole infrastructure to access freshly pumped water, with lower coliform counts, even when water was available in the waterhole. The "single-hit" epidemiological model (Haas 1983) which assumes that exposition (here ingestion) to one pathogenic organism only can be sufficient to induce disease could explain these results. Following this model, elephant drinking more water than other herbivores (from 4-fold to 40-fold increase compared to giraffe and impala respectively, Table 1), have a higher probability to ingest pathogens and develop disease than other species. This would lead elephant to drink water from the troughs, which can be more difficult to access and represent smaller areas than the remaining waterhole, but being “safer” in terms of pathogens.

However, this model does not explain patterns observed for other species. Roan and sable antelopes do not show specific patterns and have a high variability in their drinking position. The five other species (zebra, kudu, giraffe, warthog and impala) drank at locations remote from the trough, which was unexpected, especially for giraffes, which drank very far from the trough in spite of being the second species in terms of water consumption (Table 1). Haas (1983) described another less stringent model, where a minimal effective dose inherent to the organism is needed to observe infection or disease (Haas 1983). If this threshold increases with body mass, and that the quantity of pathogens ingested increase with the amount of water consumed, we would expect species consuming equivalent amount of water *per* kilogram to have the same drinking position behaviour, which is not the case (Table 1). This suggests that, if pathogen load may be an important driver of the drinking behaviour of herbivores, it is not sufficient to explain the drinking position patterns. The drinking position could therefore be the result of a compromise between pathogen avoidance and mineral requirements. Future experimental research based on choice of water of different quality and different pathogen load could help understanding the decision making of these species.

Finally, other confounding factors inherent to the waterholes could interact or override water physico-chemical characteristics to explain herbivores’ drinking position such as topography (slopes) and vegetation cover near waterholes. Indeed, the surrounding vegetation can influence perceived predation risk and can be beneficial (e.g. escape) or detrimental (e.g. camouflage for ambush predators) for herbivores (e.g. Valeix et al. 2008 and references therein). It could explain the variability between but also within waterholes, with unequal distances to cover upon the location at the waterhole. This is something that will need further investigation in the future.

4.3. Interference competition with elephants

A previous study revealed that elephants do not prevent other herbivores from drinking at waterholes (Valeix *et al.* 2009). Here, we showed that zebras and kudus drank far from the trough whether elephants are present or absent, which is not supporting a hypothesis of interference competition with elephants for the access to fresh water. The water-gradient hypothesis seems therefore unlikely to explain the spatial aggregation patterns observed by Ferry *et al.* (2016), where zebras and kudus got closer to elephants at waterholes, as the dry season progressed. Another hypothesis that has been advanced to explain the observed aggregation patterns in this previous study is that zebras and kudus get close to elephants in order to decrease their perceived predation risk, as adult elephants are almost invulnerable to predation and may sometimes deter predators. Regarding the other herbivore species, we did not highlight any interference competition for the access of fresh water as they usually drank when elephants were absent and yet they did not drink at the trough. Only sable and roan antelopes are likely to face interference competition with elephants, as they are the only ones drinking sometimes relatively close to the trough. However, sable and roan antelopes almost never drank at waterholes when elephants were present, suggesting either a temporal avoidance of elephants (Valeix *et al.* 2007) or different temporal niches at waterholes driven by other factors (e.g. food requirements, predation pressure).

	Mean drinking distance to the trough (m ± SE)	**Interval between waterhole visit (day)**	**Water consumption (litre**	**Body mass (kg)**	**Water consumption per kilograms (mililitter.kg^{-1})**
Elephant	15.4 ± 4.5	1-2 [a]	35-77 [c]	2800-6000 [d]	12.5-12.8
Roan	29.2 ± 6.0			160-230 [d]	
Sable	32.6 ± 5.1	2-4 [a]	4.6 [c]	215-300 [d]	15.3-21.4
Zebras	49.4 ± 4.7	1-2 [b]	4.7 [c]	175-320 [d]	14.7-26.9
Kudu	49.4 ± 4.0		5 [c]	170-257 [d]	19.5-29.4
Impala	53.3 ± 4.8	2-3 [c]	0.9 [c]	43-64 [d]	14.1-20.9
Giraffe	56.3 ± 5.4		10.6 [c]	450-1930 [d]	5.5-23.6
Warthog	58.6 ± 5.1			50-150 [d]	

Table 1: Characterization of the species mean drinking distance to the trough and water-dependence defined through the interval between successive waterhole visits and water consumption. [a] Cain *et al.* 2012, [b] Chamaillé-Jammes *et al.* 2014, [c] Young 1970 in Gaylard *et al.* 2003, [d] Wilson & Mittermier (2011).

Conclusion

At the end of the dry season, waterholes are characterized by heterogeneous physico-chemical characteristics of the water, with marked differences between the trough and the rest of the waterhole. In our study, we measured some physico-chemical characteristics of water but it would be interesting to identify relevant nutrient and water organoleptic properties for wildlife. Ultimately, it would help to define what a water of good quality for wildlife is. Water physico-chemical characteristics alone do not explain the observed drinking locations of herbivores, which may result from several factors. . Future experimental research controlling for water characteristics (pathogen load and mineral content) and environmental co-variables (e.g. predation pressure, topography) is required to disentangle the drivers of the drinking behaviour of large mammals at waterholes.

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Ethics

Experiments were conducted following the ARRIVE guidelines on the use of animals in research, and permits were issued by Zimbabwe Parks and Wildlife Management Authority (ZPWMA).

Authors’ contributions

NF, MC, FD, and FH collected the data; NF, SD, HF and MV designed the study, and all authors contributed to writing the manuscript, and approved the final version of the manuscript.

Competing interests

We declare we have no competing interests.

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Supporting information

Trough picture