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

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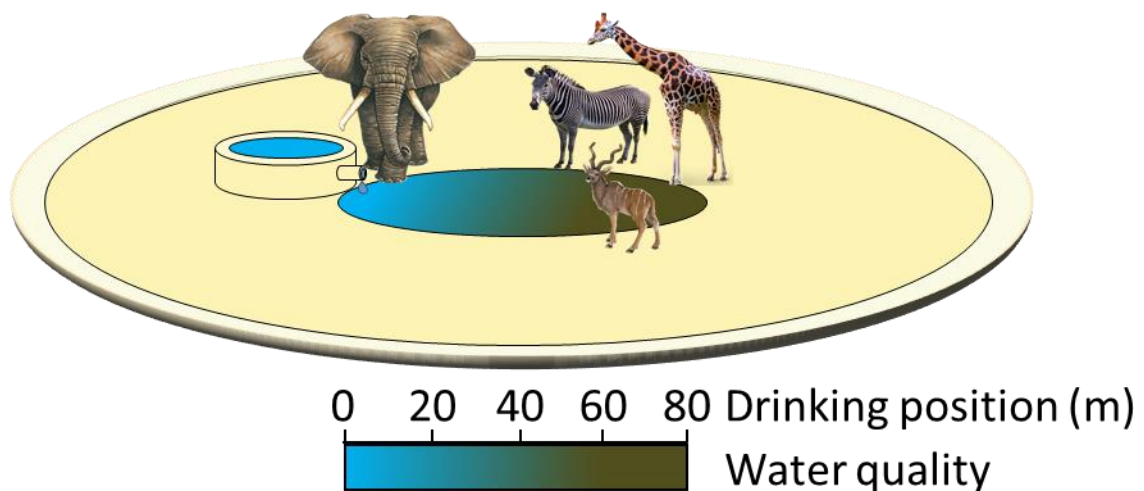
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22

23 **Abstract**

24 In many semi-arid savanna ecosystems, surface water is scarce and only found in
25 artificially pumped waterholes at the end of the dry season, leading to high large mammal
26 densities and competition. Further, the modification of the physico-chemical characteristics of
27 the drinking water over the dry season (e.g. through faeces accumulation) could enhance
28 competition. Indeed, elephants, considered as key-competitor, and other herbivores by
29 aggregating near the trough where clear water arrives could compete for this resource. We
30 studied the drinking locations of eight herbivore species around pumped waterholes in relation
31 to these water characteristics in Hwange National Park, Zimbabwe. We identified differences
32 of the physico-chemical characteristics of the water in different sections of pumped waterholes

33 at the end of the dry season. Elephants drank the water in or close to the trough, whereas other
34 species drank further in the waterhole, except roan and sable antelopes which were indifferent
35 about where they drank. Interference competition with elephants for the access to water close
36 to the trough was not detected for zebras and kudus. We discuss possible directions for future
37 research to enhance our understanding of waterhole use by herbivores.

38 **Graphical abstract**



39

40 **Highlights**

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

50

51 **Keywords**

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

54

55 **1. Introduction**

56 Species distribution patterns depend on the spatial distribution of resources (O'Neill *et al.*
57 1988, Pearson 1993). Patches of resources represent attractive areas in the landscape, around
58 which animals are likely to aggregate and may temporarily form mixed-species groups (Waser
59 1982, Stenland *et al.* 2003). The co-occurrence of different species can lead to interspecific
60 competition (exploitative or interference, Schoener 1983), forcing some species to avoid more
61 competitive ones at both spatial (Durant 2000, Tannerfeldt *et al.* 2002) and temporal scales (Ziv
62 *et al.* 1993, Valeix *et al.* 2007). The intensity of these competition processes increases as
63 resource quantity or accessibility decreases. This is typically the case of surface water resources
64 in arid and semi-arid ecosystems, where water resources dry up as the dry season progresses.
65 In many arid and semi-arid savanna ecosystems, surface water during the dry season is provided
66 mainly through artificial pumping of underground water. These pumped waterholes often
67 represent the only source of surface water available to animals at the end of the dry season. This
68 scarcity of water leads to the aggregation of a wide range of large mammal species around
69 pumped waterholes, sometimes at very high levels of abundance (Weir & Davison 1965, Valeix
70 2011).

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

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

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

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

117

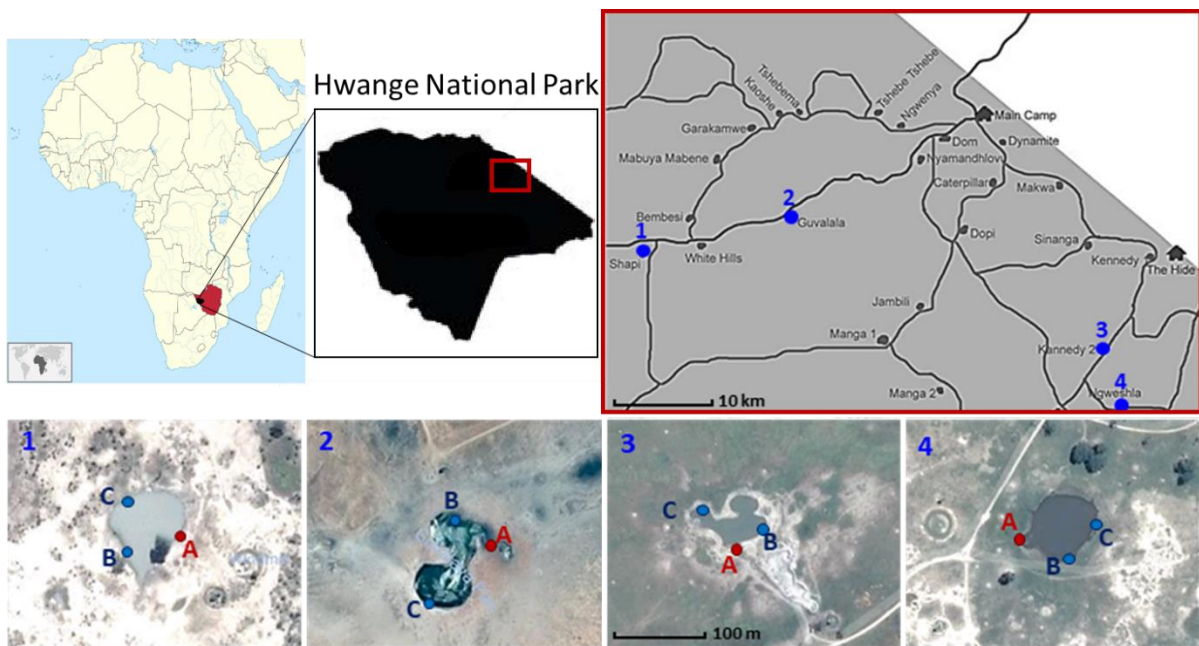
118 **2. Materials and methods**

119 2.1 Study site

120 The study area (~7 000km²) is located in the northern region of Hwange National Park which
121 covers ~15 000 km² of semi-arid dystrophic (low nutrient soil) savanna in north-western
122 Zimbabwe (19°00' S, 26°30' E; Fig. 1). The vegetation is primarily woodland and bushland
123 savanna. The long-term mean annual rainfall is ~ 600 mm, which falls primarily between
124 November and April, and the dry season stretches from May to October. The surface water
125 available to animals is found in natural waterholes and rivers as well as artificially pumped
126 waterholes. Waterholes are depressions that are fed by rainwater during the rainy season.
127 During the dry season, many waterholes are supplied with pumped underground water. Water
128 is extracted from boreholes using solar panel-powered pumps (so water is extracted during the

129 day). Water is first pumped into an open-top concrete ground-level small drinking trough, and
130 then flows continually from the trough to the depression (see Appendix 1 for pictures). Natural
131 water bodies dry up during the dry season and only artificially pumped waterholes offer
132 drinking water throughout the year and at the end of the dry season. In pumped waterholes, the
133 pumping is continuous during the day when most herbivore species come to drink (Valeix et al.
134 2007) and the waterhole is then continually fed with pumped water. Eight herbivore species
135 were monitored: two browsers (giraffe *Giraffa camelopardalis* and greater kudu), two mixed-
136 feeders (African elephant and impala *Aepyceros melampus*) two woodland grazers (roan
137 antelope *Hippotragus equinus*, and sable antelope *Hippotragus niger*) and two grassland
138 grazers (warthog *Phacochoerus africanus* and Burchell's zebra).

139



140
141 **Figure 1:** Map of the four monitored pumped waterholes in Hwange National Park, Zimbabwe.
142 Locations of B and C (in blue, corresponding respectively to locations at intermediate and the
143 longest distance from the trough) and A (in red, corresponding to the trough) for each waterhole.
144 Aerial photos of the waterholes were taken from Google Map and scale bar is the same for all
145 four waterholes.
146

147 2.2 Data

148 *2.2.1 Water physico-chemical characteristics*

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

168

169 *2.2.2 Drinking position*

170 Observations of drinking herbivores were made at the same four monitored pumped
171 waterholes (Fig. 1) between August and November 2016, i.e. at the end of the dry season. Every

172 day, observations were done from 6 a.m. until 6 p.m at one of the study pumped waterholes.
173 Observers were inside a car parked at approximately 100m from the waterhole as a
174 compromise between disturbance and quality of the observation. Each time an herbivore or a
175 group of herbivores drank at the waterhole, the position of the closest individual to the trough
176 (focal individual) was recorded. In order to calculate the distance between the drinking focal
177 individual and the trough, we recorded the angle to the north (with a compass) and the distance
178 from the car (with a range finder) of the focal individual and the trough. For all drinking
179 observations of the herbivores, we recorded if elephants were present at the waterhole or not.

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

187

188 2.3 Analyses

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

190

191 *2.3.1 Water physico-chemical characteristics*

192 In order to assess the existence of a gradient of water physico-chemical characteristics
193 inside waterholes, we performed multivariate analyses. First, a Principal Component Analysis
194 (PCA, package ade4, Dray & Dufour 2007) was performed on the thirteen variables. We then
195 removed the effect of the heterogeneity between waterholes with a within-class analysis and

196 performed a between-class analysis to estimate the percentage of the remaining variability
197 explained by the differences between the three locations A, B and C.

198

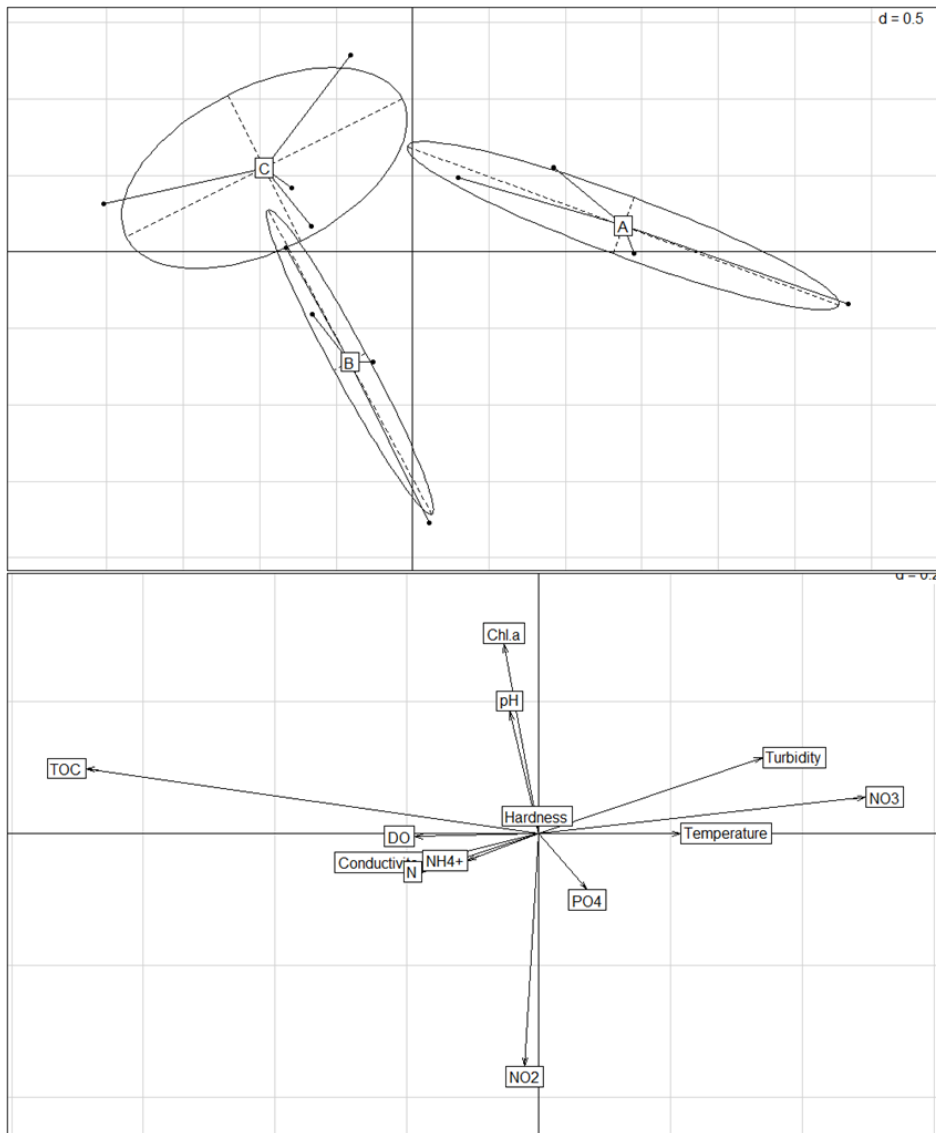
199 *2.3.2 Drinking position*

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

212 **3. Results**

213 *3.1 Water physico chemical characteristics*

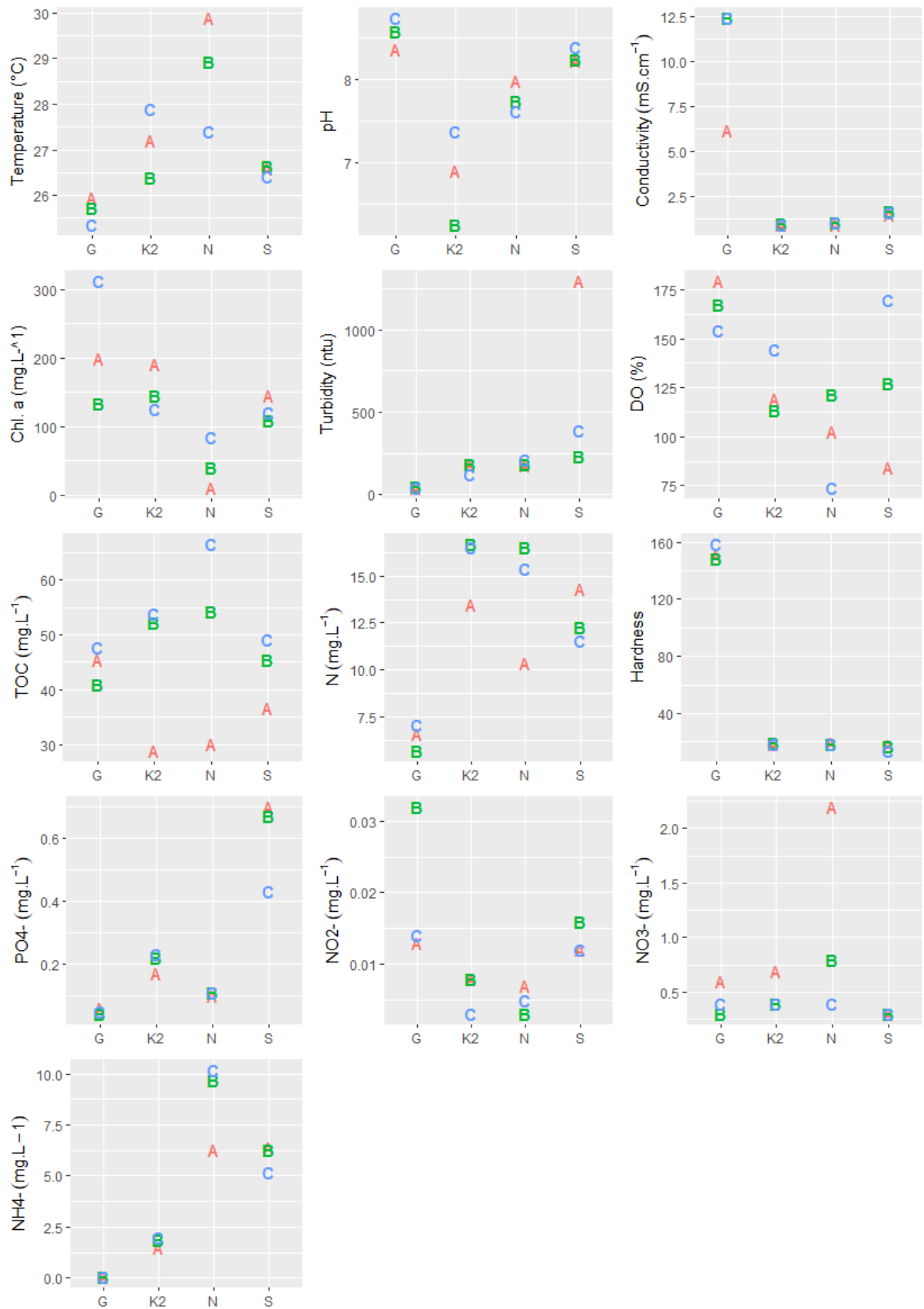
214 After the within-class analysis removed the variability due to differences between
215 waterholes, the between-class analysis revealed that 31% of the remaining variability was
216 explained by differences of water physico-chemical characteristics between the locations A, B
217 and C. As the distance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



220

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

228



229
230

Figure 3: Physico-chemical characteristics of the three points (A, B and C) respectively close,

231

intermediate and far from the trough in the four waterholes ("G" = Guvalala, "K2" = Kennedy

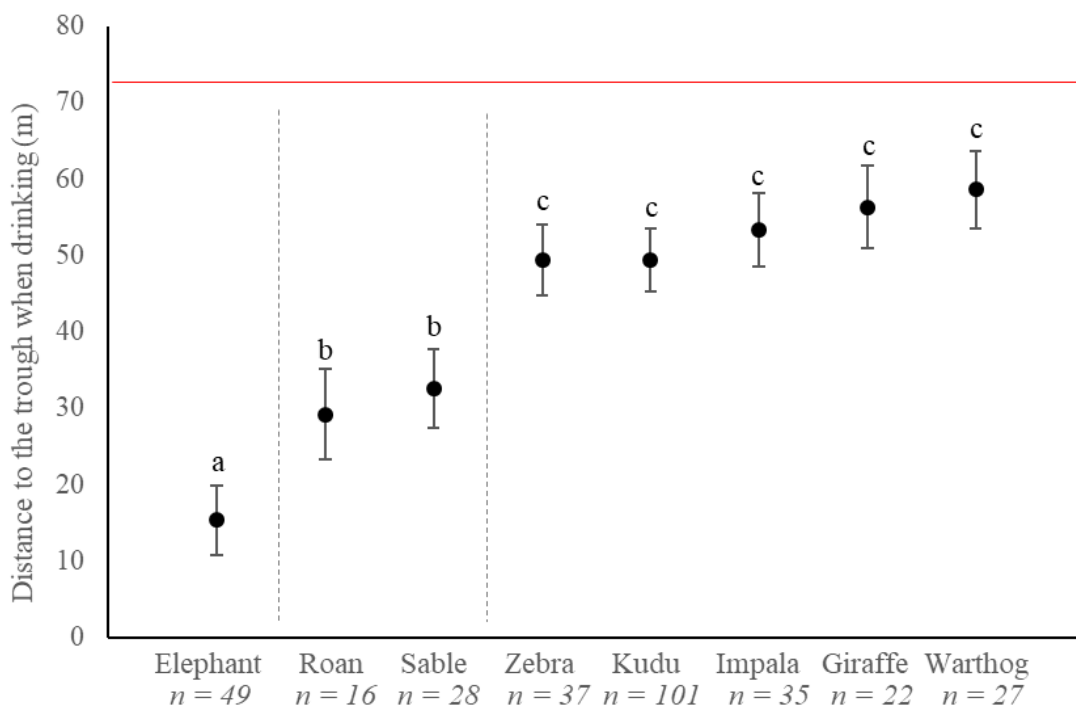
232 2, “N” = Ngweshla, “S” = Shapi). The thirteen studied physico-chemical characteristics are
233 presented: dissolved oxygen (DO), total organic carbon (TOC), total nitrogen (N), ammonium
234 (NH₄⁺), nitrite (NO₂), nitrate (NO₃), orthophosphate (PO₄) and chlorophyll a (Chl.a)
235 concentration and conductivity (Conductivity), hardness (Hardness), turbidity (Turbidity) and
236 temperature (Temperature). Regarding DWAF vol. 7 (1996) for aquatic ecosystem monitoring,
237 the target water quality range is 7 mg.l⁻¹ for ammonium (NH₄⁺), between 80 and 120% for
238 dissolved oxygen (DO) and the water is considered as hypertrophic if orthophosphate (PO₄-)
239 is above 0.25 mg.l⁻¹. Regarding DWAF vol. 1 (1996) on domestic water monitoring, if the
240 chlorophyll a (Chl.a) is above 10 mg.l⁻¹ the water “has a distinct murky appearance, becoming
241 increasingly green in colour with significant taste and odour problems and secondary growth
242 bacteria on the distribution system”, if the hardness is below 50 the water is considered as soft,
243 if it is between 150 and 200 the water is considered as “moderately hard”. Finally, if the
244 turbidity is above 10 the water carries an associated risk of disease due to infectious disease
245 agents and chemicals adsorbed onto particulate matter.

246

247

248 3.2 Drinking position

249 The mixed model allowed estimating the mean (\pm SE) drinking distance to the trough for
250 the eight study species, which ranged from 15.5 m to 58.5 m (Fig. 4). Post-hoc tests revealed
251 three different groups: (i) elephants, which drank the closest to the trough, (ii) roan and sable
252 antelopes with an intermediate estimated mean distance from the trough, and (iii) all other study
253 herbivore species (zebras, kudus, impalas, giraffes and warthogs), which drank the furthest from
254 the trough (Fig. 4). A high variability was observed between waterholes, especially for roan
255 and sable antelopes, which were observed to drink at highly variable distances from the trough
256 (Fig. 5). No effect of the presence of elephants on the drinking distance from the trough was
257 observed neither for zebras ($\beta \pm$ SE = 0.77 ± 6.56 , $t = 0.118$, $p = 0.9$), nor for kudus ($\beta \pm$ SE =
258 -1.11 ± 8.23 , $t = -0.13$, $p = 0.9$).



259

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

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



267
 268
 269

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.

270

271 **4. Discussion**

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

278 4.1. Water physico-chemical characteristics

279 Our results revealed differences of water physico-chemical characteristics in different
280 sections of pumped waterholes at the end of the dry season. Indeed, troughs are set up between
281 the outlet of the pump and the waterhole and provide water of the same characteristics as the
282 underground water to the animals because the trough is continually flushed (Wanke & Wanke,
283 2007). This water is generally less salty and conductive than surface water. Given that there is
284 no input of rainwater in the dry season, evaporation and changes due to fauna activity lead to
285 changes of the physico-chemical characteristics of the water in the waterhole (Wanke & Wanke
286 2007, Msiteli-Shumba *et al.* 2018), in particular with the concentration of ions which lead to an
287 increase in conductivity and salinity.

288 Far from the trough, the water is enriched in organic matter (high concentration of total
289 organic carbon, total nitrogen) and degradation product (ammonium). This organic matter may
290 be inherent to the presence of microorganisms in the waterhole (Strauch 2013), but also to urine
291 and faeces of the numerous animals drinking in the waterhole. This last source of contamination
292 is indeed frequently mentioned in the literature (e.g. Gereta & Wolanski 1998, Strauch 2013,
293 Hulot *et al.* unpublished data). These organic matter inputs may stimulate phytoplankton
294 growth, leading to high concentrations of chlorophyll *a* and dissolved oxygen, and lead to the

295 high turbidity and water eutrophication observed in Hwange National Park (Msiteli-Shumba *et*
296 *al.* 2018) and can intensify heterogeneity of water characteristics between trough and the
297 remaining waterhole. According to the criteria of the Department of Water and Sanitation in
298 South Africa (DWA, 1996), the water far from the trough is hypertrophic. No guideline exists
299 for wildlife concerning water quality. However, the criteria for domestic water show that the
300 high chlorophyll a concentration and turbidity are symptomatic of degraded water with
301 significant taste and odour problems, secondary bacteria growth and risk of diseases due to
302 infectious agents (DWA 1996).

303 4.2. Drinking position

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

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

320 elephant to drink water from the troughs, which can be more difficult to access and represent
321 smaller areas than the remaining waterhole, but being “safer” in terms of pathogens.

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

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

345

346 4.3. Interference competition with elephants

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

365 **Table 1:** Characterization of the species mean drinking distance to the trough and water-dependence defined through the interval between
366 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
367 Wilson & Mittermier (2011).

368 **Conclusion**

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

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395 **Ethics**

396 Experiments were conducted following the ARRIVE guidelines on the use of animals in
397 research, and permits were issued by Zimbabwe Parks and Wildlife Management Authority
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399 **Authors' contributions**

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

402 **Competing interests**

403 We declare we have no competing interests.

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406 **References**

- 407 Auer, C. (1997). Water availability and chemical water quality as important factors for
408 sustainable wildlife management in the Etosha National Park and for domestic stock in
409 farming areas of Namibia. *DEA Research Discussion Paper 26*: 1-30. Directorate of
410 Environmental Affairs, Ministry of Environment and Tourism, Namibia.
- 411 Bates, D. (2008). The lmer package for R: linear mixed-effects models using S4 classes, version
412 0.99875-9.
- 413 Cain, J. W., Owen-Smith, N., & Macandza, V. A. (2012). The costs of drinking: comparative
414 water dependency of sable antelope and zebra. *Journal of Zoology*, 286(1), 58-67.
- 415 Chamailié-Jammes, S., Fritz, H., & Holdo, R. M. (2007). Spatial relationship between elephant
416 and sodium concentration of water disappears as density increases in Hwange National
417 Park, Zimbabwe. *Journal of Tropical Ecology*, 23(6), 725-728.
- 418 Chamailié-Jammes, S., Valeix, M., Madzikanda, H., & Fritz, H. (2014). Surface Water and
419 Elephant Ecology: Lessons from a Waterhole-Driven Ecosystem, Hwange National Park,
420 Zimbabwe. *Elephants and Savanna Woodland Ecosystems: A Study from Chobe National*
421 *Park, Botswana*, 118-131.
- 422 Dray, S., & Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for
423 ecologists. *Journal of statistical software*, 22(4), 1-20.
- 424 Durant, S. M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the
425 Serengeti. *Behavioral ecology*, 11(6), 624-632.
- 426 DWAF, 1996, South African Water Quality Guidelines Volume 1 to 7 (second edition). CSIR
427 environmental Services, Holmes, S.
- 428 Epaphras, A. M., Gereta, E., Lejora, I. A., Meing'ataki, G. O., Ng'umbi, G., Kiwango, Y., ... &
429 Mtahiko, M. G. G. (2008). Wildlife water utilization and importance of artificial

430 waterholes during dry season at Ruaha National Park, Tanzania. *Wetlands ecology and*
431 *management*, 16(3), 183-188.

432 Ferry, N., Dray, S., Fritz, H., & Valeix, M. (2016). Interspecific interference competition at the
433 resource patch scale: do large herbivores spatially avoid elephants while accessing water?
434 *Journal of Animal Ecology*, 85(6), 1574-1585.

435 Gaylard, A., Owen-Smith, N., & Redfern, J. (2003). *Surface water availability: implications*
436 *for heterogeneity and ecosystem processes* (pp. 171-188). The Kruger experience: ecology
437 and management of savanna heterogeneity. Washington: Island Press.

438 Gereta, E., & Wolanski, E. (1998). Wildlife–water quality interactions in the Serengeti National
439 Park, Tanzania. *African Journal of Ecology*, 36(1), 1-14.

440 Haas, C.N. (1983). Estimation of risk due to low doses of microorganisms: a comparison of
441 alternative methodologies. *American Journal of Epidemiology*, 118(4):573–582.

442 Hayward, M. W., & Hayward, M. D. (2012). Waterhole use by African fauna. *South African*
443 *Journal of Wildlife Research*, 42(2), 117-127.

444 Hochman, V., & P Kotler, B. (2006). Effects of food quality, diet preference and water on patch
445 use by Nubian ibex. *Oikos*, 112(3), 547-554.

446 Langvatn, R., & Hanley, T. A. (1993). Feeding-patch choice by red deer in relation to foraging
447 efficiency. *Oecologia*, 95(2), 164-170.

448 Lenth, R. V. (2016). Least-squares means: the R package lsmeans. *Journal of statistical*
449 *software*, 69(1), 1-33.

450 Maseke, F. O., Abrantes, K. G., Gettel, G. M., Bouillon, S., Irvine, K., & McClain, M. E. (2015).
451 Are large herbivores vectors of terrestrial subsidies for riverine food webs? *Ecosystems*,
452 18(4), 686-706.

453 McNaughton, S. J. (1988). Mineral nutrition and spatial concentrations of African ungulates.
454 *Nature*, 334(6180), 343.

455 Msiteli-Shumba, S., Kativu, S., Utete, B., Makuwe, E., & Hulot, F. D. (2018). Driving factors
456 of temporary and permanent shallow lakes in and around Hwange National Park,
457 Zimbabwe. *Water SA*, 44(2), 269-282

458 Naiman, R. J., & Rogers, K. H. (1997). Large animals and system-level characteristics in river
459 corridors. *BioScience*, 47(8), 521-529.

460 O'Neill, R. V., Milne, B. T., Turner, M. G., & Gardner, R. H. (1988). Resource utilization scales
461 and landscape pattern. *Landscape Ecology*, 2(1), 63-69.

462 Pearson, S. M. (1993). The spatial extent and relative influence of landscape-level factors on
463 wintering bird populations. *Landscape Ecology*, 8(1), 3-18.

464 Ramey, E. M., Ramey, R. R., Brown, L. M., & Kelley, S. T. (2013). Desert-dwelling African
465 elephants (*Loxodonta africana*) in Namibia dig wells to purify drinking water. *Pachyderm*,
466 53(66), e72.

467 Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on
468 herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84(8), 2092-2107.

469 Schoener T. W. (1983). "Field experiments on interspecific competition". *The American*
470 *Naturalist*. 122 (2): 240–285.

471 Stommel, C., Hofer, H., Grobbel, M., & East, M. L. (2016). Large mammals in Ruaha National
472 Park, Tanzania, dig for water when water stops flowing and water bacterial load
473 increases. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 81(1), 21-30.

474 Strauch, A. M. (2013). Interactions between soil, rainfall, and wildlife drive surface water
475 quality across a savanna ecosystem. *Ecohydrology*, 6(1), 94-103.

476 Subalusky, A. L., Dutton, C. L., Rosi-Marshall, E. J., & Post, D. M. (2015). The hippopotamus
477 conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic
478 systems in sub-Saharan Africa. *Freshwater Biology*, 60(3), 512-525.

479 Tannerfeldt, M., Elmhagen, B., & Angerbjörn, A. (2002). Exclusion by interference
480 competition? The relationship between red and arctic foxes. *Oecologia*, 132(2), 213-220.

481 Umar, S., Munir, M. T., Azeem, T., Ali, S., Umar, W., Rehman, A., & Shah, M. A. (2014).
482 Effects of water quality on productivity and performance of livestock: A mini
483 review. *Veterinaria*, 2(2), 11-15.

484 Valeix, M., Chamaillé-Jammes, S., & Fritz, H. (2007). Interference competition and temporal
485 niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, 153(3), 739-
486 748.

487 Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F., & Madzikanda, H. (2008). The role of water
488 abundance, thermoregulation, perceived predation risk and interference competition in
489 water access by African herbivores. *African Journal of Ecology*, 46(3), 402-410.

490 Valeix, M., Fritz, H., Canévet, V., Le Bel, S., & Madzikanda, H. (2009). Do elephants prevent
491 other African herbivores from using waterholes in the dry season? *Biodiversity and
492 conservation*, 18(3), 569-576.

493 Valeix, M. (2011). Temporal dynamics of dry-season water-hole use by large African
494 herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe.
495 *Journal of Tropical Ecology*, 27(2), 163-170.

496 Van der Wal, R., Madan, N., Van Lieshout, S., Dormann, C., Langvatn, R., & Albon, S. D.
497 (2000). Trading forage quality for quantity? Plant phenology and patch choice by Svalbard
498 reindeer. *Oecologia*, 123(1), 108-115.

499 Wanke, H., & Wanke, A. (2007). Water quality for game in drylands: A case study from the
500 Khaudum National Park, Namibia. *Journal of arid environments*, 70(3), 553-559.

501 Waser, P.M. (1982) Primate polyspecific associations: do they occur by chance? *Animal
502 Behaviour*, 30(1), 1-8.

- 503 Weir, J., & Davison, E. (1965). Daily Occurrence of African Game Animals at Water Water
504 Holes During Dry Weather. *Zoologica africana*, 1(2), 353-368.
- 505 Western, D. 1975: Water availability and its influence on the structure and dynamics of a
506 savannah large mammal community. *African Journal of Ecology* 13(3-4), 265—286.
- 507 Wilmshurst, J. F., Fryxell, J. M., & Hudsonb, R. J. (1995). Forage quality and patch choice by
508 wapiti (*Cervus elaphus*). *Behavioral Ecology*, 6(2), 209-217.
- 509 Young, E. (1970). PhD. Water as faktor in die ekologie van wild in die Nasionale
510 Krugerwildtuin. English: Water as a factor in the ecology of game in the Kruger National
511 Park.
- 512 Ziv, Y., Abramsky, Z., Kotler, B. P., & Subach, A. (1993). Interference competition and
513 temporal and habitat partitioning in two gerbil species. *Oikos*, 66(2), 237-246.

514 **Supporting information**

515 Trough picture



516