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1 **Title:** Food resource competition between African wild dogs and larger carnivores
2 in an ecosystem with artificial water provision

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35

36 **Conflict of Interest**

37 None declared.

38

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43 **Authors' contributions**

44 E.S.S., M.V., E.M., E.D. and A.J.L. conceived the idea; M.M.M., S.P. and S.P.C.
45 collected and processed the scat samples; E.S.S. processed the data, did the
46 analyses, and led the writing of the manuscript; D.M, H.M and P.B supervised data
47 collection. All authors gave feedback to the drafts and final approval for publication.

48

49 **Abstract**

50 Predators of similar size often compete over prey. In semi-arid ecosystems
51 where water is a limiting resource, prey availability can be affected by water
52 distribution, which further increases resource competition and exacerbate conflict
53 among predators. This can have implications for carnivore dietary competition.
54 Hence, we evaluated the dynamics of food resource competition between African
55 wild dogs and four competing predators (cheetahs, leopards, lions and spotted
56 hyaenas) in different seasons and across areas with different waterhole densities
57 in Hwange National Park, Zimbabwe. We used the frequency of occurrence of prey
58 items found in predators' scats to analyse diet composition, overlap and prey
59 preference. For most predators, kudu was most frequently consumed and
60 preferred. Low and medium water-dependent prey (medium and small-sized) were
61 mostly consumed by wild dogs, leopards and cheetahs. Wild dog diet overlap was
62 high with all predators, particularly with hyaenas and lions. There were no seasonal
63 differences in the predators diet. The diet overlap of wild dogs with lions was
64 highest in the low waterhole density area, and wild dog diet composition did not
65 differ significantly from the diet of lions and hyaenas. In the low waterhole density
66 area, wild dogs and hyaenas broadened their niche breadth, and predators diet
67 had a higher proportion of low water-dependent prey. A low density of waterholes
68 increased food resource competition. However, high density of waterholes, where
69 there is more prey availability, can increase the aggregation and density of
70 predators, and hence, increase the risks involved in interspecific competition on
71 wild dogs. To reduce food resource competition on wild dogs, we propose to

72 conserve larger-bodied prey that are less dependent on water (e.g. kudu,
73 reedbuck, eland, gemsbok). As the use of water pumping is common practice, we
74 propose maintaining water management heterogeneity where prey which is less
75 dependent on water can also thrive.

76

77 **Keywords:** Diet, waterholes, interspecific competition, carnivores, resource
78 partitioning

79

80 **Introduction**

81 Large predators help maintain stable ecological processes as they exert top-
82 down effects (Dalerum et al. 2008). Thus, their conservation is crucial to maintain
83 healthy ecosystem functioning (Martinez-del-Rio et al. 2001). Among mammals,
84 large predators (> 21 kg) are a distinct functional group on top of the food chain
85 that can feed on a wide range of prey sizes (Radloff and Du Toit 2004). As large
86 predators belong to the same carnivorous guild, their ecological niches overlap,
87 which results in competition (Amarasekare 2003; Radloff and Du Toit 2004).

88 To promote coexistence among competing species, a form of niche
89 separation is necessary; this can be temporal, spatial or through diet partitioning
90 (Amarasekare 2003). Diet separation can reduce exploitative competition, which is
91 when species indirectly compete for common resources through depletion of these
92 resources (Tilman 1982; Ghoddousi et al. 2017). Thus, species need to adapt their
93 foraging strategies to maximize their fitness (Schoener 1971). As predators of
94 similar size compete over prey (Cupples et al. 2011; Harihar et al. 2011), a
95 subordinate predator (smaller in size) may change its diet due to the presence of a
96 dominant predator (larger in size), especially when food is scarce (Hayward and
97 Kerley 2008; Mbizah et al. 2012). In such a situation, prey selection could depend
98 more heavily on competition among predators than on predator-prey
99 characteristics (Jones and Barmuta 1998; Radloff and Du Toit 2004).

100 Diet overlap serves as an indication of resource competition (Du Preez et al.
101 2017). A high degree of diet overlap, which can indicate the potential for a high
102 level of resource competition, can exacerbate conflict among predators (Fedriani et

103 al. 2000; Donadio and Buskirk 2006; Du Preez et al. 2017). One way to reduce
104 interspecific competition is through diet segregation, particularly when competing
105 species overlap spatio-temporally (De Almeida Jácomo et al. 2004; Gerber et al.
106 2012; Balme et al. 2017). Subordinate predators can reduce interspecific
107 competition by feeding on different prey groups (e.g. prey water dependency, or
108 prey size) (Hayward and Kerley 2005; Davis et al. 2018); as well as, through
109 segregating their diet seasonally (Jones and Barmuta 1998; Carvalho and Gomes
110 2004; Azevedo et al. 2006) and spatially (different habitats and areas) (Jones and
111 Barmuta 2000; Tsunoda et al. 2019). However, it is possible that the options for
112 diet segregation are reduced when prey abundance decreases, in which case
113 subordinate predators will be affected more heavily than dominant ones (Schoener
114 1971; Creel et al. 2018; Ferretti et al. 2020; Steinmetz et al. 2020).

115 The African wild dog (*Lycaon pictus*) (~22 kg) (referred to as wild dog
116 throughout the manuscript) is an endangered, social and subordinate carnivore
117 within Africa's large carnivore guild (IUCN 2023). It suffers from interspecific
118 competition with lions (*Panthera leo*) (150-250 kg) and spotted hyaenas (referred
119 to as hyaenas throughout the manuscript) (*Crocuta crocuta*) (~70 kg). These two
120 dominant predators affect wild dogs through direct killing, exploitative competition,
121 exclusion from prey rich areas, and kleptoparasitism (Creel 2001; Van der Meer et
122 al. 2011, 2013b; Vanak et al. 2013). Wild dog diet overlaps not only with the diet of
123 lions and hyaenas, but also with the diet of leopards (*Panthera pardus*) (23-31 kg)
124 and cheetahs (*Acinonyx jubatus*) (34-64 kg) (Hayward and Kerley 2008; Mbizah et
125 al. 2012).

126 In arid and semi-arid ecosystems, water becomes a limiting resource in the
127 dry season and is therefore, in some areas, actively pumped to provide water to
128 animals (Owen-Smith 1996). Variation in water availability affects the abundance
129 and distribution of herbivores (Redfern et al. 2003; Valeix 2011), which in turn
130 affects the abundance and distribution of predators (Valeix et al. 2010, 2012), and
131 ultimately the level of intraguild competition between predators (Périquet et al.
132 2021). The widespread use of artificially supplied water in African savannahs
133 (Owen-Smith 1996; Edwards et al. 2015; Sutherland et al. 2018) can impact
134 carnivore interactions and potentially affect the fate of endangered species such as
135 wild dogs. Although food competition between large African predators has been
136 widely studied (Hayward and Kerley 2008; Mbizah et al. 2012; Creel et al. 2018),
137 the role of water on the dynamics of this competition has never been assessed.

138 Here, we aim to identify the level of food competition (diet composition, diet
139 overlap, and prey preference) between wild dogs and the four competitive
140 predators (cheetahs, leopards, lions and spotted hyaenas) in different seasons
141 (weather seasons: wet-early dry [November-June] / late dry [July-October]; wild
142 dogs' behavioural seasons: nomadic (non-breeding) [September-April] / breeding
143 (restricted in movement due to denning) [May-August]) across areas characterized
144 by contrasting water availability to assess the role of water availability, and hence
145 provisioning, on the potential exploitative competition between wild dogs and other
146 large carnivores. As water can have an impact on prey species distribution and
147 abundance, our main hypothesis is that food resource competition between wild
148 dogs with larger predators would differ between seasons and between areas with
149 different waterhole densities due to differences in prey distribution and availability.

150 We predict that the potential for resource competition, i.e. diet overlap, is higher
151 between wild dogs and the other predators during the dry and breeding season
152 and in areas with a lower density of waterholes, as prey would likely be less
153 available there.

154

155 **Methods**

156 Study site

157 The study site is situated in Hwange National Park (HNP), an unfenced
158 protected area without human settlements or paved roads and used for
159 photographic tourism. The park covers ca. 15,000 km² in western Zimbabwe
160 (19:00'S, 26:30'E) (Fig. 1), with altitudes between 800 m and 1100 m. The habitat
161 comprises of woodland, bushland and open areas of grassland mainly associated
162 with waterholes (Arraut et al. 2018). HNP does not have natural perennial water
163 sources; thus, in the dry season, animals depend on artificially provisioned
164 waterholes. The wet-early dry season (November-June) has a mean rainfall of
165 ~540 mm, and the late dry season (July-October) has a mean rainfall of ~12 mm
166 (Wilderness Safaris Zimbabwe, unpublished data for 2010-2017). During the late
167 dry season, deciduous trees lose their foliage, and pasture is of the lowest quality.
168 Waterholes are mainly found in the northern area of HNP (both in the North West
169 (NW) and North East (NE) areas - Fig. 1 - where waterhole density is 2.0 and 4.6
170 per 100 km², respectively – Table 1). The NW area has the most fertile soil (basalt
171 soil) and is characterized by woodland and bushland; while woodland and open
172 grassland in Kalahari sands characterize the NE area. Moreover, in the NW area

173 there are rivers that carry water during the wet season (Chamaillé-Jammes et al.
174 2007). The South West (SW) area is the driest part of the park (waterhole density
175 is 0.5 per 100 km²; Table 1), and characterized by bushy grassland on Kalahari
176 sand soil with almost no water provisioning during the dry season (Rogers 1993;
177 Arraut et al. 2018). Areas adjacent to HNP include human settlements, trophy
178 hunting areas and photographic safari areas (Loveridge et al. 2017). During the
179 study period in HNP (2013-2019), the density of dominant predators was estimated
180 to be: ~2.9 (± 2.2 sd) lions/100 km², and ~10.7 (± 6.1 sd) hyaenas/100 km² (Table 1;
181 Loveridge et al. 2022).

182 Data collection

183 Faecal samples of cheetahs, leopards, lions and hyaenas were collected
184 opportunistically along roads, trails, kills, and latrines from 2012 until 2015. Faecal
185 samples for wild dogs were collected while following packs from 2012 to 2020. The
186 identification of the faeces of predators was based on morphology, colour, odour
187 and associated tracks (Mbizah et al. 2012) or by directly observing defecation.
188 Following Mbizah et al. (2012), samples were photographed, washed in acetone,
189 dehydrated in 100% ethanol, and dried on filter paper. For prey species
190 identification, 6 to 8 hairs from the washed hair sample were selected from different
191 parts of the prey species' pelage. Hair cross-sections and scale pattern imprints
192 made on wood glue were photographed through a microscope and each hair was
193 identified to species level using photographic reference guides (Buys and Keogh
194 1984; Kent 2004; Seiler 2010; Taru and Backwell 2014). To limit the probability of
195 pseudo-replication, for lion and hyaena scats, we considered only one sample
196 collected per 24 hours per location (location was considered the same if ≤ 1 km

197 apart). For wild dog's scats, we considered only one sample collected per 24 hours
198 from the same pack, regardless of location. We acknowledge that there could still
199 be some pseudo-replication by only considering 24h, as complete digestion can
200 take longer, however, in order to keep a good sample size we used 24h based on
201 Mbizah et al. 2012.

202 To calculate prey abundance, we used data from line-transect surveys carried out
203 in the north of HNP in September/October (late dry season) and in May/June (early
204 dry season) each year from 2012 until 2019. Further details of line-transect survey
205 methodology in HNP can be found in Chamailé-Jammes et al. (2009). A total of
206 492 camera trap stations (Cuddeback models 1125, 1149 and C1, Non- Typical,
207 WI, USA; Panthera V4, Panthera, NY, USA; Stealthcam G42NG, Grand Praire, TX,
208 USA) were deployed between 2013 and 2020 across nine surveyed sectors (three
209 surveyed sectors per area) (total effort: 23,319 trap days). Camera trap stations
210 were placed along trails or roads and spaced in a grid of 5 km apart (Fig. 1)
211 (Loveridge et al. 2022).

212 Analyses

213 *Diet composition and comparisons*

214 To determine the diet of each predator, we analysed the faecal data as a
215 whole (including all samples: "All" category), as well as, per area (NW, NE and SW
216 areas), and per season over all years. One limitation of dividing the park into three
217 areas was that we were not able to control for instances where consumption and
218 defecation took place in different areas. However, scats collection at the margin
219 between these areas was minimal (Fig. 1). For the seasonal analyses, we took the
220 following categories into account: "wet-early dry" season (November-June) "late

221 dry” season (July-October); and “nomadic” season (September-April) when wild
222 dogs are nomadic versus “breeding” season (May-August) when wild dogs are
223 denning and therefore restricted in their movement (packs that were not denning
224 during the breeding season were excluded from this analysis: 12 scats). We
225 categorized prey species by level of water dependency (high, medium, low) and
226 diet (mixed feeder [browser and grazer], browser, grassland grazer, woodland
227 grazer, omnivorous, carnivore, other) (based on Redfern et al. 2003; De Boer et al.
228 2010; Hayward & Hayward 2012; Supporting information, Table A1). In cases
229 where we found carnivore species in the diet, they were included in the analyses
230 because even though they can be killed as part of interspecific competition, they
231 are also sometimes preyed upon by predators (Rasmussen 1996; Breuer and
232 Breuer 2005; Du Preez et al. 2017). We used prey size based on mean female
233 weight as described by Cumming & Cumming (2003) and Kingdon (2004) (XS
234 extra-small <5 kg, S small 6-24 kg, M medium 25-99 kg, L large 100-349 kg, XL
235 extra-large >350 kg) (Mbizah et al. 2012; Balme et al. 2017) (Supporting
236 information, Table A1). Wild dogs hunt together as a pack which allows them to
237 increase hunting efficiency and to hunt for larger prey (Creel and Creel 1998). To
238 determine if there was any correlation of wild dog pack size with prey size, we
239 performed a Cumulative Link Mixed Model - CLMM (*ordinal* package; Christensen
240 2022), using prey size as the dependent variable, pack name as a random factor,
241 and pack hunting size (excluding pups) as a fixed factor. As the distribution of prey
242 weights was clumped, we used prey weight class, a categorical variable, and
243 hence used ordinal regression: CLMM.

244 To determine if we collected the minimum number of scats needed to
245 adequately describe the diet of predators, we calculated prey-species
246 accumulation curves using the function *specaccum* in the *vegan* package
247 (Oksanen et al. 2018) (Supporting information, Fig. A1). Because of a small
248 sample size (< 21) neither cheetah's diet (information only available for the NW
249 area) nor leopard diet in NE and seasonally were included in statistical
250 comparisons, as we did not perform any analysis when there were less than 21
251 scats within a category (Supporting information, Table A2a).

252 For each area and season, we calculated the frequency of occurrence
253 (Klare et al. 2011). For the "All" category, we also estimated the relative biomass
254 intake. Following Woodroffe et al. (2007), we used the Weaver's equation derived
255 from the grey wolf (*Canis lupus*): prey mass per scat (kg) = 0.439 + (0.008 * prey
256 species' mean female weight) to estimate the biomass intake for wild dogs
257 (Weaver 1993). Following Briers-Louw (2017) and Du Preez et al. (2017), we used
258 the Ackerman's equation derived from pumas (*Puma concolor*) for the other
259 predators: prey mass per scat (kg) = 1.980 + (0.035* prey species' mean female
260 weight) (Ackerman et al. 1984). As these formulas are not specific for the species
261 of our study, the biomass results are only indicative representations of the
262 proportions of biomass consumed and not necessarily the accurate biomass value.
263 When calculating biomass, we corrected for the maximum stomach capacity of
264 each predator, which were corrected at a maximum of 10 kg for leopards, 24 kg for
265 hyaenas and 50 kg for lions (Kruuk 1972; Bertram 1975). As the highest biomass
266 consumed per scat for wild dogs and cheetahs (4 kg) did not exceed maximum
267 stomach capacity (~9 kg) (Creel and Creel 1995), there was no need to correct

268 their biomass calculations. For seasonal and spatial comparisons on predators diet
269 composition, we performed a permutational analysis of variance (PERMANOVA) of
270 prey species found in the predators' scats with 1000 permutations and controlling
271 for "year" using the *adonis2* function of the *vegan* package (Oksanen et al. 2018).
272 We used PERMANOVA analysis because it is a non-parametric test that compares
273 groups' differences where it is possible to stratify the permutations performed
274 (Oksanen et al. 2018). This meant that we were able to control for "year" in our
275 comparisons. When comparing prey species composition, we used the Jaccard
276 index (presence/absence data: prey species in each scat): $J = \frac{A+B-2J}{(A+B-J)}$; where A
277 and B are the numbers of species in compared predator scats, and J is the number
278 of species shared in predator scats (Jaccard 1908). When comparing prey
279 categories (prey water dependency, prey diet and prey size), we used the Bray-
280 Curtis dissimilarity index (using abundance data, as more than one prey species
281 could be found in each category): $= \frac{\sum_{i=1}^n |X_{ij}-X_{ik}|}{\sum_{i=1}^n (X_{ij}+X_{ik})}$; where X_{ij} and X_{ik} are the
282 numbers of prey species per category i found in predator scats j and k ; n is the
283 number of categories (Bray and Curtis 1957).

284 As this is a study using scats and not direct observations, we were not able
285 to determine the proportion of prey consumed through scavenging or hunting;
286 however, it is mainly lions and hyaenas that scavenge or kleptoparasitize if the
287 opportunity appears, wild dogs very rarely scavenge (Creel and Creel 2002;
288 Périquet et al. 2015).

289 *Diet overlap and niche breadth*

290 To determine the diet overlap of wild dogs with the other predators, we used

291 Pianka's index (Pianka 1973): $O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$; where O_{jk} is the diet overlap

292 between predators j and k ; p_{ij} is the prey proportion i of the total prey used by

293 predator j ; p_{ik} is the prey proportion i of the total prey used by predator k ; and n is

294 the total number of prey items. This index ranges between 0 (no overlap) and 1

295 (complete overlap). For seasonal diet overlap, we only included the samples

296 collected in the northern part of HNP, as in the SW no wild dog samples were

297 collected in the wet-early dry seasons and there was no breeding information on

298 wild dogs available. We evaluated statistical significance of Pianka's index with a

299 null model in which diet items are reshuffled randomly and independently (with

300 10,000 iterations) while maintaining the observed prey species richness. For this,

301 we used the *EcoSimR* package (Gotelli et al. 2015). To determine the diet niche

302 breadth of each of the three predators, we used the standardized Levin's index

303 (Levins 1968; Krebs 1999): $B = \frac{1}{\sum p^2}$, and $Bs = \frac{B-1}{n-1}$, where B is niche breadth; p is

304 the proportion of prey items; Bs is standardized niche breadth; and n is the total

305 number of prey. Both diet overlap and niche breadth indexes were calculated taking

306 into account all consumed prey by all predators.

307 *Prey preference*

308 To determine whether prey consumption was based on prey availability or

309 prey preference, we used Jacobs' index: $D = (r - p)/(r + p - 2rp)$, where r is

310 the proportion of prey in the diet and p is the proportion of prey available. A Jacobs'

311 index value of -1 indicates maximum avoidance and a value of +1 maximum

312 preference (Jacobs 1974). We calculated Jacobs' index using two different
313 measurements for prey availability (that we calculated): 1) prey density, and 2)
314 prey relative abundance index (RAI). Prey density is a more accurate measure for
315 prey abundance, however RAI was also used, as prey density was not available in
316 the SW of HNP. To coincide with the sampling period of scat collection of
317 predators, we calculated prey abundance data from all years (2012-2019) to
318 calculate prey preference of wild dogs, and prey abundance data of 2012 to 2015
319 to calculate prey preference of the other predators. To calculate prey density, we
320 used distance sampling methods (Buckland et al. 2001) using the *Distance*
321 package (Miller 2020). We used 5% truncation, and ran models using half-normal,
322 uniform, and hazard-rate key-functions with cosine/polynomial series expansion,
323 both including and excluding vegetation type as a covariate for detection function.
324 We selected the model with the smallest Akaike Information Criterion (Burnham
325 and Anderson 2002), and checked the goodness of fit with a chi-square test
326 (results of p-value were above 0.20). To calculate prey RAI, we used camera trap
327 data and calculated RAI as follows: independent records / trap-days. We used as
328 independent records, consecutive photographs of different individuals (appearing
329 on the same picture together) of the same species taken more than 30 minutes
330 apart (O'Brien et al. 2003). We calculated RAI indexes per survey sector and then
331 averaged the indexes per area. Prey densities can be found in Supporting
332 information, Table A3; and prey RAI can be found in Supporting information, Table
333 A4. We considered that there was statistical evidence of a difference when a p-
334 value was over 0.05; and we performed all our analyses using R 4.1.2 (R Core
335 Team 2022).

336

337 **Results**

338 *Diet composition and comparisons*

339 In total, for wild dogs, there were 225 food items sampled in 209 scats with
340 20 prey species identified; for cheetahs, 27 items in 26 scats and 7 species; for
341 leopards 246 items in 204 scats and 25 species; for lions there were 351 items in
342 342 scats and 33 species; and for hyaenas there were 337 items in 317 scats and
343 33 species (Supporting information, Table A2a). Main results are summarized in
344 Table 2.

345 There was no evidence of seasonal differences (either in wet-early dry vs.
346 late dry [pseudo- $F_{2,839} = 1.14$, $p = 0.59$], or in nomadic vs. breeding; [pseudo- $F_{1,815} =$
347 0.64 , $p = 0.16$]) in the diet of wild dogs, lions and hyaenas (Supporting information,
348 Table A5a). However, there was evidence that predators diet differed in different
349 areas of the park (Table 3; Supporting information, Table A5b).

350 Overall, the most frequent prey species (by occurrence) for wild dogs were
351 impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), duiker
352 (*Sylvicapra grimmia*) and bushbuck (*Tragelaphus scriptus*) (~94% of total diet;
353 where kudu and impala encompassed ~66% of the diet). In terms of biomass, kudu
354 was the prey species with the highest contribution to the wild dog diet (~40%)
355 followed by impala (~33%). For cheetahs, the most common prey were scrub hare
356 (*Lepus saxatilis*), impala, duiker (*Sylvicapra grimmia*) and bushbuck (~80%), and
357 impala the most important in terms of biomass (~37%). For leopards, the most
358 common prey were duiker, bushbuck and steenbok (*Raphicerus campestris*)
359 (~51%), and kudu the most important in terms of biomass (~20%). For lions,

360 impala, kudu, buffalo (*Syncerus caffer*) and sable (*Hippotragus niger*) were the
361 most common prey species (~42%), while the prey with the highest biomass
362 contributions were buffalo, eland (*Taurotragus oryx*) and elephant (*Loxodonta*
363 *africana*) (~42%). For hyaenas, the most important prey species both in terms of
364 frequency and in terms of biomass were impala, kudu and sable (~42%); and in
365 addition to these species, buffalo was important in terms of biomass (~16%) (Fig.
366 2; Supporting information, Fig. A2).

367 Only in the low waterhole density area there was no statistical evidence that
368 wild dog diet differed from the diet of both lions and hyaenas, this was consistent in
369 terms of diet composition (lion: pseudo- $F_{1,74} = 1.079$, $p = 0.33$; hyaena: pseudo-
370 $F_{1,129} = 1.56$, $p = 0.068$), in terms of prey water dependency (lion: pseudo- $F_{1,483} =$
371 6.91 , $p = 0.70$; hyaena: pseudo- $F_{1,461} = 7.91$, $p = 0.25$) and prey size (lion: pseudo-
372 $F_{1,74} = 1.54$, $p = 0.21$; hyaena: pseudo- $F_{1,129} = 1.62$, $p = 0.20$). Contrarily, in the high
373 waterhole density area, wild dog diet differed significantly from the diet of the other
374 three predators in terms of diet composition, prey diet and prey size, but not in prey
375 water dependency. Leopard diet composition was different from the diet of wild
376 dogs in the areas tested (NW and SW), except in terms of prey diet and prey size
377 in the low waterhole density area (Table 4, Supporting information, Tables A5b and
378 A6).

379 Wild dog diet differed significantly between the high waterhole density area
380 (NW) and the maximum waterhole density area (NE) in composition (pseudo-
381 $F_{1,167} = 4.14$, $p = 0.004$), prey water dependency (pseudo- $F_{1,167} = 4.65$, $p = 0.0012$),
382 and prey size (pseudo- $F_{1,167} = 4.61$, $p = 0.015$) (Supporting information, Table A5b,
383 and A6). Wild dogs had a higher proportion of impala (medium mixed feeder) in

384 their diet in the maximum waterhole density area (NE), a higher proportion of kudu
385 (large browser) in the high waterhole density area (NW), and a more diverse diet in
386 the low waterhole density area (SW), including duiker and steenbok (Fig. 3). For
387 lions there was some evidence that they had differences in their diet between the
388 different areas ($p = 0.057$), for the other predators there was no evidence for
389 differences in their diet in the different areas (Supporting information, Table A5b).
390 However, when comparing prey water dependency in their diet, lions and hyaenas
391 had a higher proportion of less water-dependent prey in the low waterhole density
392 area (lion: pseudo- $F_{1,191} = 19.74$, $p = 0.012$; hyaena: pseudo- $F_{1,292} = 17.73$, $p =$
393 0.002), such as kudu and duiker for lion diet and duiker for hyaena diet (Table 3,
394 Fig. 3; Supporting information, Fig. A3, Tables A7 and A8).

395 Overall, wild dogs had a higher frequency of high and low water-dependent
396 species (which also are medium mixed and browsing feeders) in their diet. We did
397 not find any correlation of wild dog pack size with prey size (estimate = -0.02 (SE =
398 0.027); $p = 0.45$). Cheetahs and leopards consumed the highest proportion of low
399 water dependent prey species (which also are small and medium mixed and
400 browser species); whereas lions and hyaenas consumed a high frequency of
401 water-dependent species (which also are large and medium grassland grazers and
402 mixed feeders) in their diet (Supporting information, Fig. A4).

403 *Diet overlap and niche breadth*

404 In total, wild dog diet overlap was high with all predators (>0.55), but higher
405 with hyaenas (0.85) and lions (0.71) (Supporting information, Table A2b; Fig. 4).
406 There was more diet overlap between wild dogs and predators in the high and low
407 waterhole density areas than in the maximum waterhole density area. In the low

408 waterhole density area, wild dog and lion diet overlapped the most, while in the
409 high waterhole density area wild dog and hyaena diet overlapped the most (Fig. 4).
410 All Pianka's indices were significantly different from null models ($p < 0.05$). Overall,
411 wild dogs had the narrowest niche breadth of the five predators. However, in the
412 low waterhole density area, wild dogs had the broadest diet niche (Fig. 4).

413 *Prey preference*

414 Kudu (medium water-dependent prey), duiker and bushbuck (low water-
415 dependent prey) were preferred by wild dogs, cheetahs and leopards in all areas.
416 In addition, leopards preferred impala, steenbok, sable, waterbuck (*Kobus*
417 *ellipsiprymnus*), wildebeest (*Connochaetes taurinus*) and giraffe (*Giraffa*
418 *camelopardalis*). Lions and hyaenas preferred duiker, wildebeest, waterbuck,
419 sable, eland, reedbuck (*Redunca arundinum*) and warthog (*Phacochoerus*
420 *africanus*); and hyaenas also preferred kudu and giraffe. Only in the maximum
421 waterhole density area wild dogs preferred waterbuck. In general, prey density and
422 prey RAI gave similar results. Prey RAI results showed that most prey were less
423 abundant in the low waterhole density area (Table 1, Supporting information, Table
424 A4a). However, when we calculated Jacobs' index using prey density, buffalo was
425 not preferred, and impala was only preferred in the maximum waterhole density
426 area; but when using prey RAI both prey species were preferred (density values
427 were higher than RAI values for both species) (Fig. 5; Supporting information, Fig.
428 A5).

429

430 **Discussion**

431 Artificial water provisioning in arid and semi-arid ecosystems is a common
432 practice throughout Africa (Owen-Smith 1996; Edwards et al. 2015; Sutherland et
433 al. 2018). As water distribution can affect herbivores availability and abundance
434 (Redfern et al. 2003; Valeix 2011), the competition level of predators over prey can
435 also be affected. In HNP, competition over prey was high between wild dogs and
436 larger predators (cheetahs, leopards, lions, hyaenas), and the levels of food
437 resource competition between wild dogs with dominant predators (lions and
438 hyaenas) differed between areas with different waterhole densities associated to
439 different levels of resource availability.

440 *Diet composition*

441 Wild dog diet overlap was high with all predators. Overall, it was highest with
442 hyaenas, similar to findings from Breuer and Breuer (2005) and Mbizah et al.
443 (2012), and lowest with leopard and cheetah diet. This contrasts with other studies
444 where wild dog diet overlapped more with cheetah and leopard diet than with lion
445 and hyaena diet (Hayward and Kerley 2008; Vogel et al. 2019). This might indicate
446 that wild dogs are subjected to higher levels of dietary competition with the two
447 most dominant predators (lions and hyaenas) in HNP than in other parts of Africa.
448 This could add competition pressure of dominant predators to wild dogs in HNP.

449 Wild dogs, cheetahs and leopards preyed more upon less water-dependent
450 species (which are mixed, browser, medium and smaller species). While, lions and
451 hyaenas preyed more frequently upon high water-dependent species (which are
452 grazers and larger sized species). These differences in prey categories could
453 facilitate coexistence.

454 Contrary to our predictions that food resource competition was going to be
455 different between seasons, season did not influence diet composition of predators
456 nor the level of resource competition between wild dogs with lions and hyaenas. In
457 HNP, Davidson et al. (2013), also found that overall there were no seasonal
458 differences in lion diet. In other carnivores and ecosystems, there were seasonal
459 foraging differences that depended on seasonal food availability (Padial et al.
460 2002; Lanszki et al. 2020; Vissia et a. 2022). Our results demonstrate that the level
461 of resource competition did not depend on prey fluctuation due to seasonality, as
462 waterholes are also pumped in the dry season. Perhaps, instead of seeking
463 different prey in different seasons, wild dogs focused on different age and sex
464 classes of the same species (Pole 2000), depending on the breeding season of
465 their main prey.

466 The main prey of wild dogs were impala, kudu, duiker and bushbuck. These
467 results are consistent with other studies in HNP (Childes 1988; Van der Meer et al.
468 2013b) and other areas (Pole et al. 2004; Hayward et al. 2006; Mbizah et al. 2012).
469 However, impala was not always preferred by wild dogs, but consumed according
470 to availability. Prey size tends to increase with wild dog pack size (Creel and Creel
471 1995), but we did not find a correlation with pack size and prey size. This result
472 could be because we did not consider prey age classes, or because even only one
473 individual wild dog can kill large prey species such as a kudu (PDC unpublished
474 data). In densely vegetated areas, wild dogs hunting success is higher (Creel and
475 Creel 2002), and the risk of kleptoparasitism is lower (Creel and Creel 1996, 1998).
476 Therefore wild dogs may prefer to make their kills in dense vegetation where

477 kudus, bushbucks and duikers (as strict browsers) are commonly found (Valeix et
478 al. 2009).

479 *Resource competition in areas with different waterhole densities*

480 In the low waterhole density area, the level of resource competition of wild
481 dogs with lions and hyaenas was higher. This was mainly due to both dominant
482 predators shifting their diet (lion and hyaena diet had a higher proportion of wild
483 dogs preferred prey species in this area). Only in this area, wild dogs diet did not
484 differ from lion and hyaena diet, nor did it differ in terms of prey diet and size with
485 leopard diet (browsers were consumed more by the four predators). Browsers are
486 less dependent on water than grazers (Redfern et al. 2003; Valeix 2011), which
487 could also explain why browsers were consumed more in the low waterhole density
488 area. In this area, wild dogs and leopards had a higher proportion of duiker and
489 steenbok in their diet; hyaenas consumed proportionally more duikers compared to
490 other areas; and lions consumed a significantly higher proportion of low water-
491 dependent species (kudu, duiker, steenbok) than in other areas of HNP. For both
492 dominant predators, in the driest area, there is less abundance of preferred prey,
493 which are mainly large sized, grazers, and high water-dependent prey; this can
494 explain why lions and hyaenas consume more prey preferred by wild dogs (prey
495 smaller in size and less water dependent) in that area. All this potentially indicates
496 a high level of resource competition between wild dogs with both dominant
497 predators (especially with lions) in the area with the lowest waterhole density.

498 Wild dogs had the largest niche breadth in the low waterhole density area. In
499 this area, wild dogs preferred prey included a wider range of prey species (i.e.
500 sable, reedbuck, gemsbok [*Oryx gazelle*] and baboon [*Papio ursinus*]), which were

501 avoided in the high and maximum density areas, possibly because these species
502 are more dangerous to hunt (Van der Meer et al. 2019). Wild dogs would tend to
503 evade hunting these species to avoid any potential fitness costs imposed by
504 hunting dangerous prey. Carnivores need to become more generalist when there is
505 lower prey abundance (Macarthur and Levins 1967; Lanszki et al. 2019), especially
506 subordinate carnivores competing with dominant ones for food (Dröge et al. 2017;
507 Petroelje et al. 2021). Consequently, wild dogs might have had to broaden their
508 niche breadth in this area to compensate for a high diet overlap with the dominant
509 predators, as well as, due to a lower relative prey abundance.

510 *Conservation implications*

511 It is important to conserve complete predator guilds to preserve ecological
512 processes (Dalerum et al. 2008). Although wild dogs are adapted to coexist with
513 other predators as they have evolved with them for millennia (Turner 1990), water
514 provisioning could potentially aggravate the interspecific competition of wild dogs
515 by reducing areas to escape competition inside protected areas with high dominant
516 predator densities and outside protected areas with high anthropogenic threats
517 (Van der Meer et al. 2013a).

518 Wild dogs might not necessarily need an exclusive prey species to survive,
519 as kudu, impala and duiker are also important prey for the four other predators,
520 and bushbuck is a species also preferred by leopards and cheetahs. However, a
521 reduction of prey abundance can increase food resource competition (Karanth and
522 Sunquist 1995; Creel et al. 2018; Sévêque et al. 2020), which is what seems to be
523 happening in the low waterhole density area in HNP.

524 Although wild dogs do not seem to be limited by prey availability (Creel and
525 Creel 1998; Woodroffe et al. 2007), reducing prey availability can affect wild dogs
526 by increasing intraguild competition (Creel et al. 2018). Moreover, low prey
527 abundance could affect wild dogs' reproduction (Marneweck et al. 2019b),
528 potentially increase intraspecific competition between African wild dog packs
529 (Marneweck et al. 2019a), and increase the probability of packs consuming
530 livestock herewith provoking conflict with humans (Woodroffe et al. 2005).

531 It is crucial to conserve both density and diversity of prey, especially prey
532 preferred by threatened predators (Hayward and Kerley 2008; Davidson et al.
533 2019). Kudu is an important species because it was preferred, and had frequency
534 and high biomass contribution in the diet of most predators (especially in wild dog
535 diet). In the low waterhole density area with high resource competition, and where
536 lions and hyaenas were consuming a higher proportion of smaller prey less
537 dependent on water (possibly because there was less abundance of large bodied
538 prey), conserving large sized prey preferred, like eland and gemsbok, by lions and
539 hyaenas, would most likely decrease the food competition on wild dogs. Hence, we
540 emphasise not only to prioritize the conservation of kudu, but also the conservation
541 of other large prey species moderately dependent on water, such as reedbuck,
542 eland and gemsbok, mainly in areas with low waterhole density. This is consistent
543 with Creel et al. 2018 who found that a lack of large bodied prey leads to more
544 dietary competition. Hence, we propose to conserve these prey species by keeping
545 their populations stable but not necessarily increasing their abundance. To
546 prioritize the conservation of these prey species we recommend to avoid the culling
547 of them, as well as to have enough spaces without too many waterholes: either by

548 closing waterholes in the maximum waterhole density area, or by not creating more
549 waterholes in areas with high waterhole densities.

550 In high waterhole density areas, there is a higher density of dominant
551 predators (Loveridge et al. 2022), which means that there is a higher number of
552 competitors for food in those areas. Moreover, if prey abundance is high (such as
553 in high waterhole density areas), dominant carnivores' density can increase
554 (Carbone and Gittleman 2002; Hayward et al. 2007), and have negative effects on
555 wild dogs (Creel and Creel 1996, 1998), such as excluding them from prey rich
556 areas (Creel 2001), or even through direct mortality (Prugh and Sivy 2020). When
557 food resource competition is high, diet partitioning might not play a major role in
558 predators' niche segregation for coexistence. Instead, in those cases,
559 spatiotemporal dimensions might be the main mechanisms allowing coexistence,
560 such as wild dogs hunting in crepuscular times and dominant predators hunting at
561 night, or by wild dogs avoiding areas highly used by lions (Bruno et al. 2003; Dröge
562 et al. 2017; Tsunoda et al. 2019; Vissia et al. 2022).

563 Low waterhole density in the ecosystem increases food resource
564 competition (especially with lions); but high waterhole density in the ecosystem
565 (where there is more prey availability), can increase the density of predators
566 (Macdonald 2016), and hence, increase the risks involved in interspecific
567 competition on wild dogs (Creel 2001). Thus, we emphasize the need to maintain
568 heterogeneity in water management actions.

569 *Conclusion*

570 Resource competition between wild dogs with larger predators, driven by
571 fluctuations of prey availability and abundance, differed between areas with

572 different waterhole densities, but not between seasons. Dietary competition of wild
573 dogs with dominant predators (especially with lions) was highest in the low
574 waterhole density area. To reduce food resource competition (exploitative
575 competition) on wild dogs, we propose to conserve larger-bodied prey that are less
576 dependent on water. As food resource competition was high between wild dogs
577 with the four larger predators, spatiotemporal partitioning might be playing a major
578 role to allow coexistence.

579

580 **Conflict of Interest**

581 None declared.

582

583 **Data Availability Statement**

584 The data is available in:

585 [https://figshare.com/articles/dataset/Sandoval_Seres_et_al_2024_Food_resource_](https://figshare.com/articles/dataset/Sandoval_Seres_et_al_2024_Food_resource_competition_between_African_wild_dogs_and_larger_carnivores_in_an_ecosystem_with_artificial_water_provision_csv/25112936)
586 [competition_between_African_wild_dogs_and_larger_carnivores_in_an_ecosyste](https://figshare.com/articles/dataset/Sandoval_Seres_et_al_2024_Food_resource_competition_between_African_wild_dogs_and_larger_carnivores_in_an_ecosystem_with_artificial_water_provision_csv/25112936)
587 [m_with_artificial_water_provision_csv/25112936](https://figshare.com/articles/dataset/Sandoval_Seres_et_al_2024_Food_resource_competition_between_African_wild_dogs_and_larger_carnivores_in_an_ecosystem_with_artificial_water_provision_csv/25112936)

588 doi: 10.6084/m9.figshare.25112936

589

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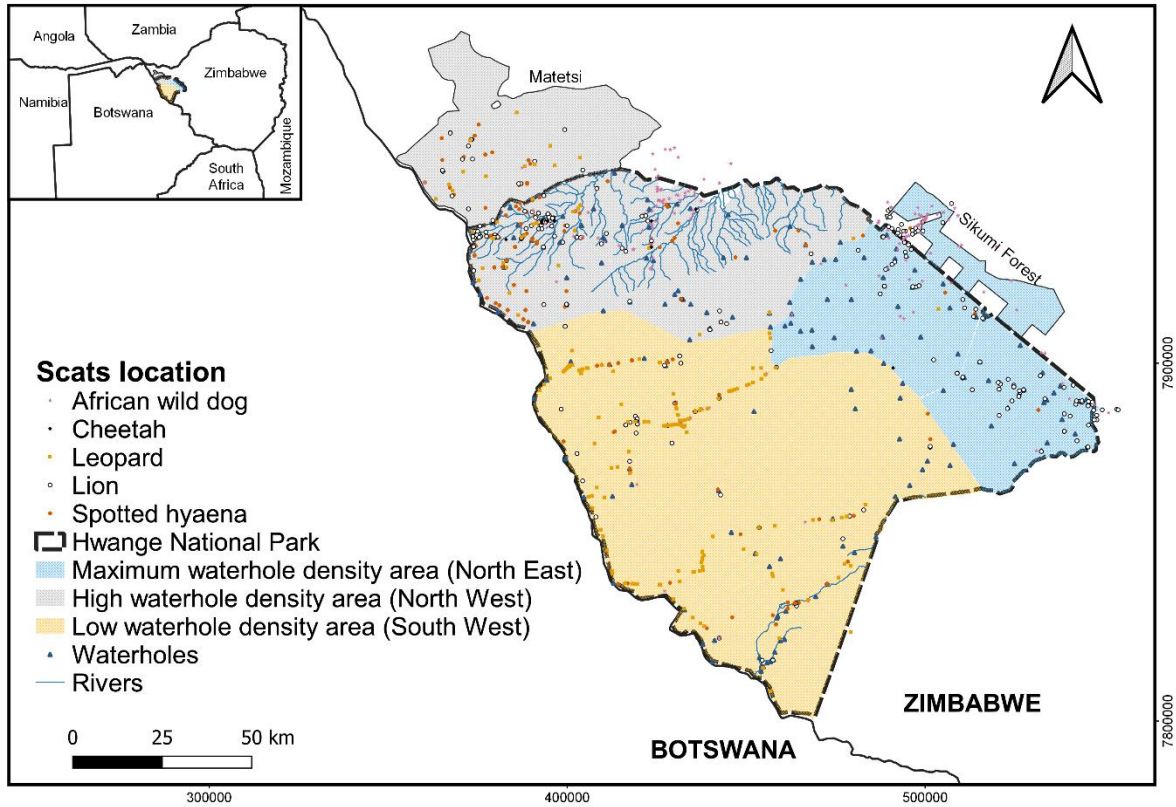
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916 **Figures:**

917 **Figure 1** Map of the study area, Hwange National Park, Zimbabwe, with locations
918 of scat samples per predator within the three areas of the park with contrasting
919 waterhole densities.



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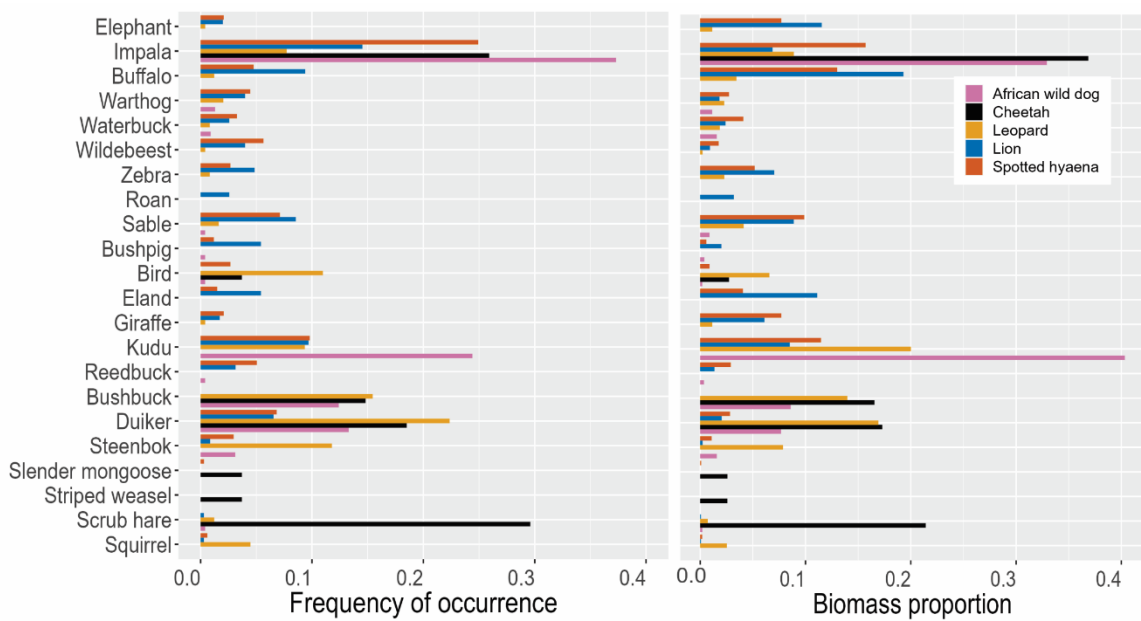
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927 **Figure 2** Frequency of occurrence and biomass proportion of prey species for the
 928 five large carnivores in Hwange National Park, Zimbabwe. Only including species
 929 with either frequency of occurrence or biomass larger than 0.03. Supporting
 930 information, Fig. A2 includes all species. Order from high water-dependent prey to
 931 low water-dependent prey.

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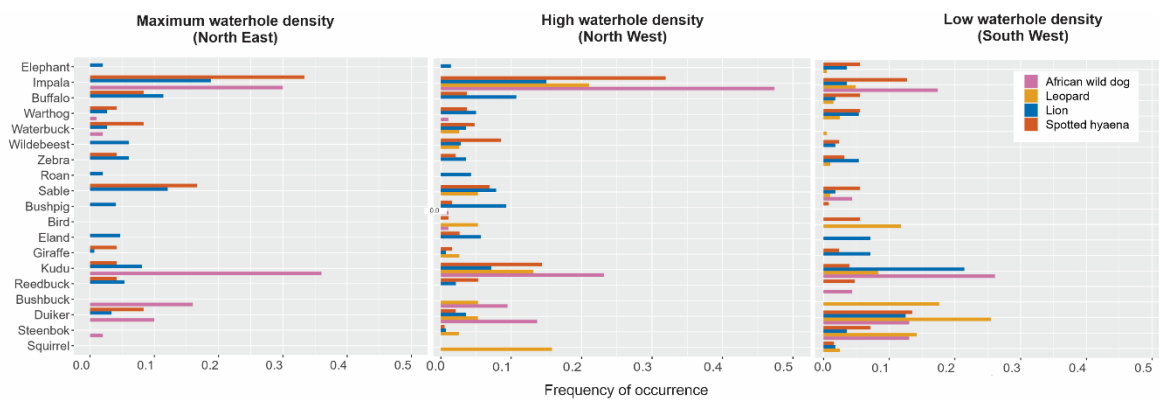
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940 **Figure 3** Frequency of occurrence per area of the proportions of the main prey in
 941 the diet of four predators in three different areas of Hwange National Park,
 942 Zimbabwe. Prey species are ordered by size. Only including species with the
 943 frequency of occurrence larger than 0.03. Supporting information, Fig. 3 includes
 944 all species. Order from high water-dependent prey to low water-dependent prey.

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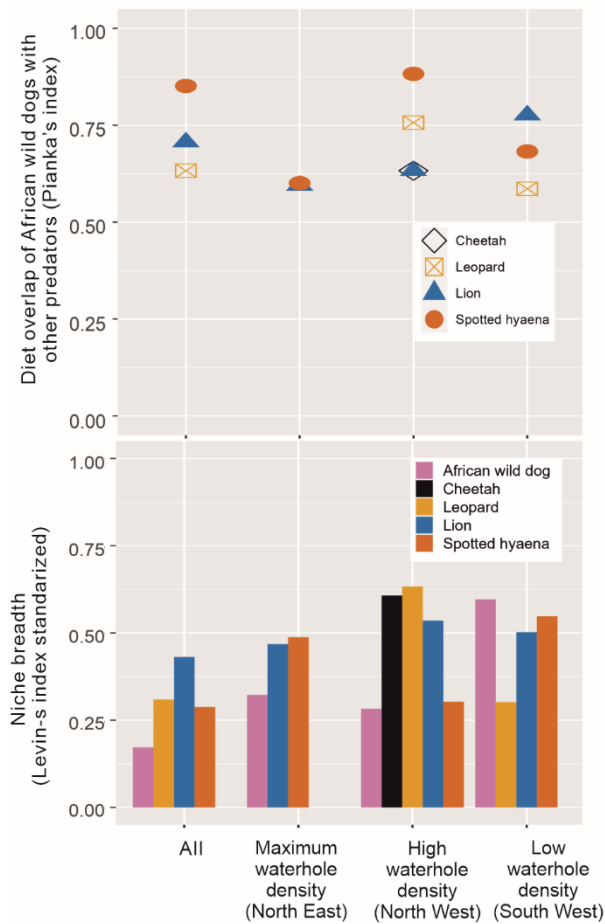
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955 **Figure 4** Diet overlap and dietary niche breadth of five predators in three different
 956 areas of Hwange National Park, Zimbabwe. Indexes are calculated including
 957 carnivores in the predators diet. Data on cheetahs only in North West, no data of
 958 leopards in North East.

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964 **Figure 5** Diet preference (Jacobs' Index calculated with RAI – relative abundance
 965 index) of five predators in three different areas of Hwange National Park,
 966 Zimbabwe. NE = North East (Maximum waterhole density area); NW = North West
 967 (High waterhole density area); SW = South West (Low waterhole density area).
 968 Supporting information, Fig. A5 has the diet preference with Jacobs' Index
 969 calculated with prey density.

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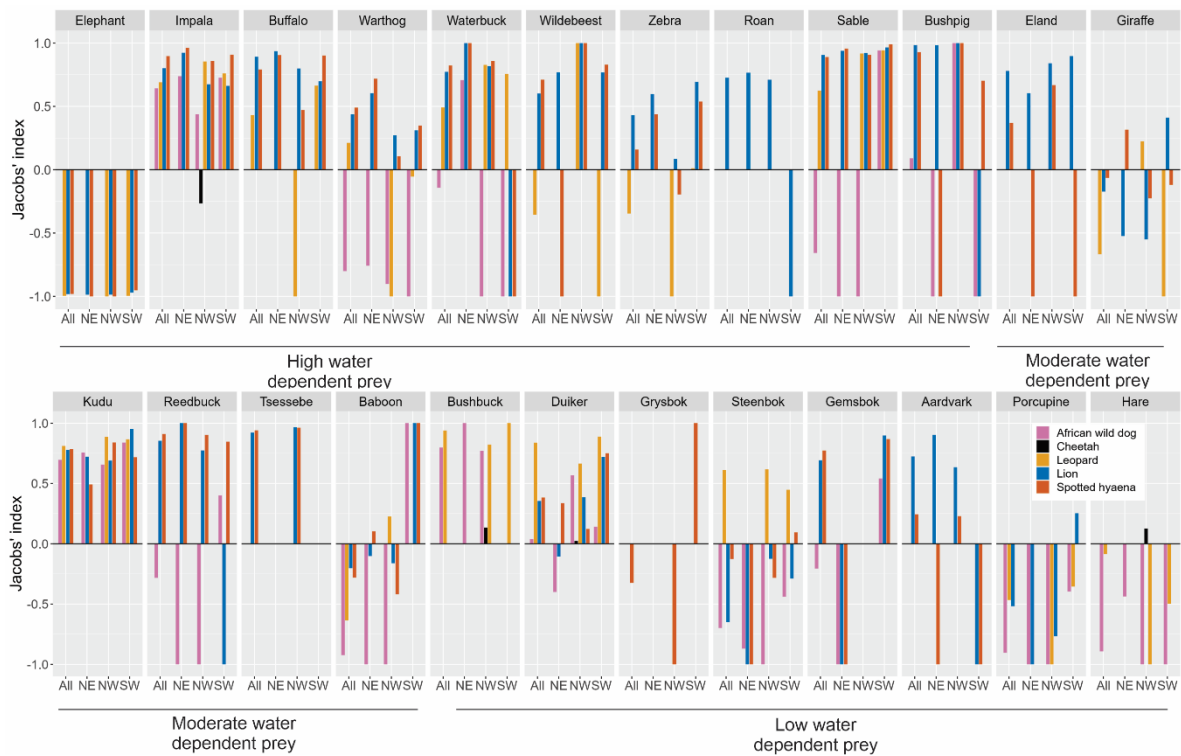


Table 1. Characteristics of the study areas in Hwange National Park, Zimbabwe.			
Areas	North East	North West	South West
Waterhole density per 100 km ²	~4.6	~2.0 + seasonal rivers	~0.5
Vegetation types and soil	Woodland, open grassland, bushed grassland on Kalahari sand soil.	Woodland, grassland, and bushland on basalt soil (most fertile).	Bushed grassland on Kalahari sand soil.
Average abundance of African wild dogs (2014-2020) (±SE standard error)	Pack size = ~7.5 (±0.6) Pack number = ~10.0 (±1.3)	Pack size = ~10.9 (±1.0) Pack number = ~7.9 (±1.3)	Pack size = ~8.3 (±2.3) Pack number = ~2.2 (±0.7)
Average densities (2013-2019) per 100 km ² (±SD standard deviation)	Leopard ~2.3 (±1.0) Lion ~2.3 (±1.3) Spotted hyaena ~8.4 (±2.1)	~3.0 (±1.5) ~6.5 (±0.3) ~19.1 (±5.4)	~2.0 (±0.1) ~1.8 (±1.1) ~6.1 (±1.1)
Summary of prey species abundances[#]	Highest for: duiker, steenbok, wildebeest, sable, kudu, elephant, and zebra.	Highest for: impala, buffalo, bushbuck, kudu, warthog.	Low, except for gemsbok, bushpig and reedbuck.

Vegetation and soil taken from Arraut et al. (2018).

African wild dogs' abundance including pups less than 1-year-old (PDC Annual Reports).

Predator densities taken from Loveridge et al. (2022).

[#]Prey density and relative abundance index taken from Supporting information, Table 3 and 4.

Table 2. Predators diet results summary.

	Maximum waterhole density area	High waterhole density area	Low waterhole density area
African wild dog main prey	Kudu, bushbuck and waterbuck.	Impala and bushpig.	Duiker and steenbok .
Cheetah main prey	No data.	Bushbuck, duiker and scrub hare.	No data.
Leopard main prey	No data.	Impala , kudu and squirrel.	Duiker , bushbuck, steenbok and birds.
Lion main prey	Impala, buffalo and sable.	Buffalo and bushpig.	Kudu and duiker .
Spotted hyaena main prey	Impala and sable.	Kudu, impala and wildebeest.	Duiker and steenbok .
Diet overlap of African wild dogs with lions	0.59	0.63	0.77
Diet overlap of African wild dogs with spotted hyaenas	0.60	0.88	0.68

Main prey refers to most common and preferred.

In bold = shared prey species between African wild dogs and other predators per area, and the highest diet overlap.

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Table 3. Differences on prey water dependency in the diet of predators in areas with contrasting waterhole densities in Hwange National Park, Zimbabwe.

	Maximum vs. High waterhole density area	High vs. Low waterhole density area	Maximum vs. Low waterhole density area
African wild dog	pseudo-F _{1,167} = 4.65 p = 0.0012* r ² = 0.027	pseudo-F _{1,99} = 4.35 p = 0.51 r ² = 0.042	pseudo-F _{1,108} = 0.92 p = 0.25 r ² = 0.008
Leopard	NA	pseudo-F _{1,199} = 14.56 p = 0.26 r ² = 0.068	NA
Lion	pseudo-F _{1,285} = 0.41 p = 0.62 r ² = 0.0014	pseudo-F _{1,191} = 19.74 p = 0.012* r ² = 0.094	pseudo-F _{1,202} = 23.23 p = 0.048* r ² = 0.103
Spotted hyaena	pseudo-F _{1,205} = 1.32 p = 0.34 r ² = 0.0064	pseudo-F _{1,131} = 19.74 p = 0.081 r ² = 0.094	pseudo-F _{1,292} = 17.73 p = 0.002* r ² = 0.057

NA = not applicable due to lack of data.

*In bold = statistical evidence for significant results (p < 0.05)

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Table 4. Differences between the diet of African wild dogs with the diet of other predators in Hwange National Park, Zimbabwe.

	African wild dog vs.		
	Maximum waterhole density area	High waterhole density area	Low waterhole density area
Leopard	NA	pseudo-F _{1,113} = 5.66 p = 0.0019* r ² = 0.048	pseudo-F _{1,185} = 3.15 p = 0.0059* r ² = 0.017
Lion	pseudo-F _{1,236} = 12.77 p < 0.001* r ² = 0.051	pseudo-F _{1,216} = 13.89 p < 0.001* r ² = 0.06	pseudo-F _{1,74} = 1.079 p = 0.33 r ² = 0.014
Spotted hyaena	pseudo-F _{1,110} = 4.96 p = 0.24 r ² = 0.043	pseudo-F _{1,262} = 6.99 p < 0.001* r ² = 0.026	pseudo-F _{1,129} = 1.56 p = 0.072 r ² = 0.012

NA: not applicable due to lack of data.

*In bold = statistical evidence for significant results (p < 0.05)

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