

1 **Omnivores and browsers are more resilient than mixed feeders and grazers**
2 **to human induced surface water scarcity in Ruaha National Park, Tanzania**

3
4
5 **Abstract**

6 In Africa, burgeoning human populations promote agricultural expansion and the associated
7 demand for water. Water abstraction for agriculture from perennial rivers can be detrimental
8 for wildlife, particularly when it reduces water availability in protected areas. Ruaha National
9 Park in southern Tanzania, one of the largest parks in Africa, contains important wildlife
10 populations, including rare and endangered species. The Great Ruaha River is the main dry
11 season water source for wildlife in the Park. Water offtake from this river for large-scale
12 irrigation and livestock production up-stream of the Park has caused large expanses of this
13 formerly perennial river within the Park to dry up during the dry season. We investigated how
14 available surface water during the dry season affected the distribution of ungulate species.
15 During three dry seasons (2011-2013), we determined locations of surface water and
16 collected spatial data for nine ungulate species by driving standardized ground transects,
17 including a 104 km section of the Great Ruaha River. The dietary niche hypothesis predicts a
18 functional relationship between mammalian herbivore diets and their dependence on surface
19 water, and thus the distance maintained to surface water during the dry season. Distance
20 maintained to water should increase from grazers (buffalo, waterbuck, plains zebra) to mixed
21 feeders (elephant, impala), to browsers (giraffe, greater kudu) to omnivores (warthog,
22 common duiker). Functional responses of herbivores, as analysed by a generalised linear
23 mixed effects model, demonstrated that during the dry season, distance to water was (i)
24 shortest in buffalo and waterbuck (grazers), (ii) similar for plains zebra (grazer), elephant and
25 impala (mixed feeders), (iii) larger in giraffe and greater kudu (browsers) and (iv) largest in
26 omnivores (warthog, common duiker). These findings demonstrate substantial species

27 differences in surface water dependence that are broadly in line with predicted species
28 resilience to anthropogenic reduction in surface water in Ruaha National Park.

29

30 **Keywords:** water dependence, herbivore dietary niche, surface water, irrigation, Great
31 Ruaha River, Ruaha National Park

32

33 **Introduction**

34 Surface water is utilised by humans for many purposes, including crop irrigation, livestock
35 production and electricity generation (Lemly et al 2000; Malmqvist and Rundle 2002;
36 Dudgeon et al. 2006) and this can have negative ecological effects on water sources both
37 locally and on a larger scale (Pringle 2001; Higgisson et al. 2018). In Africa, accelerating
38 demand for freshwater by the burgeoning human population (Roberts 2011, Gerland et al.
39 2014), threatens river systems and the biodiversity they support (Pringle 2001; Dudgeon et al.
40 2006; Vörösmarty et al. 2010). Conflicts over access to water resources is increasing in
41 Africa (Ashton 2002) and agricultural demand for water is rising sharply, particularly for
42 large-scale crop irrigation (Johansson et al. 2016; Ogutu et al. 2016; Rockström and
43 Falkenmark 2016).

44 There are examples in Africa where human activities both within and outside protected areas
45 have altered the natural flow of rivers, thereby challenging the biological integrity of
46 protected areas (Pringle 2001). For example, long-term, intensive abstraction of water from
47 perennial rivers upstream of the Kruger National Park in South Africa, for irrigation and
48 other activities, reduced river flow within the park, which created ephemeral rivers and
49 lowered the water table, resulting in the death of riparian vegetation and the alteration of
50 animal distributions (Pringle 2001). To ameliorate the problem of reduced surface water,
51 more than 300 artificial permanent water sources were constructed, which further altered

52 animal distribution in the Park (Pringle 2001; Redfern et al. 2003; Smit et al. 2007). Artificial
53 water sources increased the density of grazers (plains zebra, *Equus quagga*, and wildebeest,
54 *Connochaetes taurinus*) in regions of the park that were the former stronghold of locally
55 endangered roan, *Hippotragus equinus*. The roan population then crashed with the likely
56 proximate cause being increased predation by lions (*Panthera leo*) attracted by increased
57 densities of plains zebra and wildebeest and the ultimate cause, the creation of artificial
58 waterholes, which resulted in an influx of prey (Harrington et al. 1999).

59 Surface water is lost because of evaporation during African dry seasons as there is little or no
60 rainfall for several months. Consequently, the location of natural sources of surface water
61 changes as the dry season progresses (Redfern et al. 2005, Stommel et al. 2016a). In
62 response, water dependent ungulate species aggregate in areas close to available sources of
63 surface waters (Western 1975; Thrash et al. 1995; Owen-Smith 1996; Redfern et al. 2003;
64 Chamaillé-Jammes et al. 2007; Veldhuis et al. 2019; Roug et al. 2020), and predators are
65 drawn to these aggregations of prey (Fischhoff et al. 2007; Valeix et al. 2009). The distance
66 ungulate species range from available sources of surface water during dry seasons provides a
67 measure of their dependence on water (Kay 1997).

68 The degree of water dependence in mammals is shaped by a range of factors such as diet,
69 digestive physiology, temperature regulation mechanisms, body size and the loss of water via
70 faeces and urine (Taylor et al. 1969; Western 1975; Redfern et al. 2003; Redfern et al. 2005;
71 Chamaillé-Jammes et al. 2007; Kihwele et al. 2020). In terms of diet, grazers are considered
72 more water dependent than browsers because the moisture content of grasses is typically less
73 than that of browse during the dry season (Western 1975). This suggests that grazers should
74 remain at a shorter distance to surface water during the dry season than browsers. Omnivores
75 that consume underground plant structures such as tubers, rhizomes and fruits that contain
76 more water than plant matter consumed by either grazers or browsers in the dry season

77 should be less dependent on surface water than either grazers or browsers. In terms of
78 digestive physiology, hindgut fermenters, such as equids, have a high throughput of forage
79 and produce more moist faeces than ruminants, thus plains zebra should require more water
80 than similar sized ruminants (Cain et al. 2012). Species such as the waterbuck (*Kobus*
81 *ellipsiprymnus*) that cannot concentrate urine when short of water and maintain their body
82 temperature within a narrow limit by sweating and panting (Spinage 2013) should be more
83 water dependent than species that can concentrate urine and tolerate a far larger variation in
84 body temperature before temperature regulation mechanisms are required. These dietary
85 niches in combination with physiological traits should be reflected in the spatial distribution
86 of feeding guilds of African ungulates and define their vulnerability to climatic events such as
87 prolonged dry seasons and droughts.

88 The main source of surface water for wildlife in Ruaha National Park (NP), in central
89 Tanzania, is the Great Ruaha River (Mtahiko et al. 2006). Large scale abstraction of water
90 from this river for irrigation upstream of the National Park is considered responsible for the
91 substantial decline in dry season flow since the early 1990s, and the drying up of large
92 sections of this formerly perennial river within the Ruaha NP during the dry season (Mtahiko
93 et al. 2006). The decline in flow of the Great Ruaha River during the dry season leads to
94 stagnation of surface water in shrinking pools and poor water quality in terms of an increase
95 in salinity and bacterial load (Stommel et al. 2016a). The drying up of large sections of the
96 river substantially alters the distribution of the populations of common hippopotamus
97 (*Hippopotamus amphibius*, Stommel et al. 2016b) and African buffalo (*Syncerus caffer*, Roug
98 et al. 2020). Currently, little is known about the impact of water abstraction from the Great
99 Ruaha River on wildlife in Ruaha NP, particularly on water dependent species during the dry
100 season. As a result, the possible consequences for these species of any future increase in

101 water abstraction upstream of the Park or any further reduction in surface water due to
102 climate change is difficult to predict.

103 The aim of our study was to investigate the functional relationship of water dependence to the
104 diet of the nine most numerous mammalian herbivore species in Ruaha NP during the dry
105 season, and the response of these species to the decline in the availability of surface water as
106 the dry season progressed. We hypothesized that diet affects distance to the nearest source of
107 surface water and used this measure as an index of water dependence. We also used this
108 measure as a possible index of species vulnerability to future reduction of surface water
109 availability in Ruaha NP, if water abstraction increases with human population growth
110 (Roberts 2011), and/or annual precipitation declines as some climate change scenarios for
111 East Africa predict (Chen and Georgakakos 2015; Rowell et al. 2015).

112

113 **Methods**

114 *Study site*

115 The study was conducted during three dry seasons (2011-2013) within Ruaha NP in central
116 Tanzania (Fig. 1). Ruaha NP was established in 1964. It was expanded in 2008 to include the
117 Usangu Game Reserve, making it one of the largest (20,226 km²) national parks in Africa
118 (Mtahiko et al. 2006). Thus the Eastern Usangu wetland, which is an important biodiversity
119 hotspot and an important source of water for the Great Ruaha River, gained increased
120 protection. Before this, the Eastern Usangu wetland experienced substantial encroachment by
121 livestock that caused habitat degradation and a reduction in water retention. Until the early
122 1990s, the section of the Great Ruaha River (GRR) through Ruaha NP and associated
123 protected areas had running water throughout the year, except for a brief period in 1954. By
124 1993, the GRR had become an ephemeral river; this decline was chiefly due to large scale
125 water abstraction for rice production upstream of the National Park (Mtahiko et al. 2006).

126 The study area (Fig. 1) is described in detail by Stommel et al. (2016a) and details on the
127 spatial and temporal distribution of surface water for each year of the study are provided
128 elsewhere (Stommel et al. 2016b). In brief, in all years of the study at the beginning of the
129 dry season in June, the entire course of the GRR within the study area contained flowing
130 water. Surface water also occurred in depressions filled by rain and at discrete locations in
131 ephemeral tributaries and at several natural springs elsewhere. We collectively term sources
132 of surface water that were not in the GRR as non-GRR water sources (Stommel 2016a,
133 2016b). At the start of the dry season, all rain-filled depressions dried out quickly. Some
134 locations in ephemeral rivers and the springs in the study area retained water throughout one
135 or more dry seasons (Stommel 2016a, 2016b). In all years of the study, water levels in the
136 GRR decreased throughout the dry season, river flow had stopped by the end of August, and
137 stretches of the riverbed were mostly dry by September, except for a few drying pools in the
138 riverbed along the furthest downstream section in the northeast of Ruaha NP (Fig. 1). As the
139 dry season progressed, surface water continued to decline and further sections of the river
140 dried out. By October, in all years of the study, most of the downstream section of the GRR
141 was dry, apart from a few pools.

142 *Data collection and study species*

143 Ten ground transects (hereafter called transects) were conducted twice per month from June
144 to October and once in November during the three dry seasons 2011, 2012 and 2013 along
145 existing wildlife viewing tracks (Fig. 1), resulting in 11 weeks of sampling per year. These
146 were divided into early (June-Aug, 6 sampling weeks) and late dry season (Sept-Nov, 5
147 sampling weeks). Each transect was approximately 20 km (mean transect length $19,880 \text{ m} \pm$
148 115.3 m [standard error of mean, S.E.M.]) in length, and included five transects along the
149 GRR (transects 6, 7, 8, 9 and 10), and five perpendicular transects leading away from the
150 main river bed (transects 1, 2, 3, 4 and 5, Fig. 1). Transects were further classified into

151 upstream (1, 2, 3, 6, 7; “Jongo”), midstream (4, 8, 9; “Mdonya”) and downstream (5, 10;
152 “Lunda”) sections. This resulted in six compartments of different desiccation stages from wet
153 to dry (Fig. 2): upstream-alongside (U-A, transects 6 and 7), upstream-perpendicular (U-P,
154 transects 1-3), midstream-alongside (M-A, transects 8 and 9), midstream-perpendicular (M-P,
155 transect 4), downstream-alongside (D-A, transect 10) and downstream-perpendicular (D-P,
156 transect 10).

157 Data along transects were collected between 07:00 and 11:00 hours in the morning. Sightings
158 of the nine most numerous species of herbivore were recorded, including African buffalo,
159 waterbuck (*Kobus ellipsiprymnus*), plains zebra (*Equus quagga*), giraffe (*Giraffa*
160 *camelopardalis*), greater kudu (*Strepsiceros zambesiensis*) (hereafter kudu), impala
161 (*Aepyceros melampus*), elephant (*Loxodonta africana*), warthog (*Phacochoerus africanus*)
162 and common duiker (*Sylvicapra grimmia*). We did not include the hippopotamus
163 (*Hippopotamus amphibious*) because this species’ dependence on sources of surface water in
164 Ruaha NP is reported elsewhere (Stommel et al. 2016b). To avoid bias caused by differences
165 in the probability of detecting animals in different habitat types, only observations of animals
166 located within 100 m of each transect were used because animals at this distance could be
167 sighted regardless of habitat type. For each sighting of an animal or a group of animals, the
168 perpendicular distance between the animal or group to the transect was measured with a laser
169 range finder (Bushnell, PinSeeker 1500 (7x26)), and the number of animals per species seen
170 was recorded. The GPS coordinates (latitude, longitude) of the location of each animal or
171 group were taken as the perpendicular position of the vehicle on the transect line. As the
172 maximum distance for recording any animal to the right and left of the vehicle along all
173 transects was set at 100m, this method resulted in a maximum bias of ± 100 m for locations.
174 The distribution of available surface water was monitored from the beginning to the end of
175 the dry season as detailed by Stommel et al. (2016a), resulting in a record with available

176 surface water sources throughout the dry season. We computed the Euclidean distances (m)
177 from the transect location of all animals or groups to the nearest available source of surface
178 water (hereafter termed distance to water) using the statistical software package R, version
179 4.2.1 (R Core Team 2022) and ArcGIS version 10.3.1 (ESRI Inc., Redlands, CA, USA).
180 Therefore, increasing distances from animals to the next water source are a sign of increasing
181 desiccation in case of sedentary animals that are territorial or bound to their dens (e.g.
182 common duiker or warthog), or a sign of coping (physiological and/or behavioural flexibility)
183 with water scarcity.

184 *Dietary categories of herbivores*

185 Several aspects have been used to categorise the diet of African herbivores, including
186 anatomy, behavioural observations and stable isotope analyses of tissue, teeth or faeces
187 (Hofmann and Stewart 1972; Jarman 1974; McNaughton and Georgiadis 1986; Gagnon and
188 Chew 2000; Cerling et al. 2003; Codron et al. 2007). Defining categories is problematic for
189 some species because of differences in diet across habitats or seasons. For example, impala
190 can change from a predominantly grass diet during wet periods to a diet dominated by browse
191 during dry periods (e.g., Cerling et al. 2003; Copeland et al. 2009). The dietary categories we
192 assign to species in this study are broad and based on the expected diet of each species in the
193 dry season. Even so, we recognise that dietary categories occur along a continuum and a
194 species category might change with habitat.

195 African buffalos are typically considered grazers of grasses and sedges even though they
196 occasionally browse. They prefer grass species with moderate protein levels and avoid plant
197 species of low nutritious quality or the presence of aromatic oils (Redfern et al. 2003).

198 Waterbuck are considered grazers because their diet is dominated by grass (Cerling et al.
199 2003; Sponheimer et al. 2003) even though waterbuck may browse in the late dry season or
200 early wet season (Spinage 2013). Grass dominates the diet of plains zebra, thus zebras are

201 considered to be grazers (Cain et al. 2012). Giraffe are browsers that feed on deciduous trees,
202 particularly *Acacia* species, shrubs and vines during the wet season, and on evergreen species
203 near rivers during the dry season. It is thought that giraffe obtain water from plants and dew,
204 and as a result may be relatively independent of surface water, even though they do drink
205 from sources of surface water (Redfern et al. 2003; Ciofolo and Le Pendu 2013). Greater
206 kudus are typically classed as browsers (Redfern et al. 2003). They consume mostly
207 deciduous woody plants, forbs, fruits, seedpods and succulent leaves of *Euphorbia* and *Aloe*
208 species. Grasses are a minor component of their diet (Owen-Smith 2013). Impala in East
209 Africa are considered mixed feeders (Gagnon and Chew 2000; Cerling et al. 2003) as they
210 browse and graze during the wet season and in some habitats predominantly browse during
211 the dry season (Fritz and Bourgarel 2013). Elephants are mixed feeders as they consume both
212 grass and browse. They vary the proportion of these types of forage in their diet to obtain the
213 highest ratio of protein to fibre, and also consume woody vegetation and the leaves and bark
214 of certain tree species (Poole, Kahumbu and Whyte 2013).

215 Although a stable isotope study categorised warthogs as hyper-grazers (Harris and Cerling
216 2002) and the wet season diet of this species is mostly grass, the dry season diet of warthogs
217 includes rhizomes, fruits, tree pods, tubers, bulbs, carrion and the predation of small
218 mammals (Radke 1985; Wilson 1975; Blair 2012; Cummings 2013). We therefore classified
219 warthogs in Ruaha NP as omnivorous during the dry season. As the diet of the common
220 duiker consists mostly of browse, fruits, flowers, fallen leaves, small herbs, seeds, carrion and
221 young birds (Wilson 2001, Wilson 2013) we also classified this species as an omnivore. In
222 summary, for the dry season of Ruaha NP we categorised African buffalo, waterbuck and
223 plains zebra as predominantly grazers, giraffe and greater kudu as predominantly browsers,
224 impala and elephant as mixed feeders and warthog and common duiker as omnivores.

225 *Statistical analysis*

226 The following analyses were conducted using R version 4.2.1 (R Core Team 2022). We used
227 a generalised linear mixed-effects model framework (GLMM) to investigate factors that best
228 explained the distance of species to the nearest source of surface water (distance to water;
229 response variable). Predictors included species identity (species) and day of the dry season
230 with the start of the dry season set to 1st of June (juldate). Transects were classified into either
231 perpendicular or leading alongside the GRR (transect_GRR) or belonging to the desiccation
232 direction from downstream to upstream (river_class). We further accounted for the number of
233 individuals in a group counted per sighting (species_count). Year and transect-ID were
234 included as random effects.

235 Before fitting the model, we checked for linearity by exploring the shape of the response for
236 each species in relation to 'juldate' with a generalised additive model (GAM, package
237 'mgcv', Wood 2006) using a negative binomial error distribution with log-link function and
238 an interaction term between species and juldate. Visual inspection of the smoothed variable
239 did not show any deviation from linearity, apart from buffalo and zebra, which however had
240 huge confidence intervals (Supplement Fig. S1). To avoid overdispersion, we fitted negative
241 binomial models using the family 'nbinom2' in the R package 'glmmTMB' (Brooks et al.
242 2017; VerHoef et al. 2007). We tested several models with increasing complexity, i.e.
243 considered the above mentioned variables additively or in interaction with species identity,
244 and used AIC to rank the models. We selected the final model based on the lowest AIC and
245 used the R package 'DHARMA' for model diagnostics (Hartig 2022). The data set and data
246 analysis code are provided under [*github repository provided on acceptance*].

247

248 **Results**

249 The total number of animals of each species observed bi-weekly along transects, mean bi-
250 weekly group sizes and their associated mean bi-weekly distances by transect class (alongside

251 vs. perpendicular) are presented in Table 1. Information about bi-weekly total counts per
252 river class (upstream to downstream) in the early and late dry season is provided in Fig. 2.
253 Except for warthog in the early dry season and common duiker, all animals were sighted
254 alongside GRR transects (Fig. 2). The three grazers were never observed in the dry
255 perpendicular downstream section, the mixed feeders (impala, elephant) only occasionally.
256 Buffalo counts were much higher in the early than late season alongside the river; their
257 numbers collapsed during the late dry season as they leave the study area, so only a few were
258 recorded in the downstream transects in the late dry season (Figs. 2 and 3, Supplement Fig.
259 S2). In general, buffalo and impala counts were much higher than the counts of other species,
260 and common duiker sightings were rare. Group sizes, i.e. counts of individuals per sighting,
261 differed between early and late dry season, depending on species, with impala, greater kudu
262 and waterbuck slightly increasing group sizes and giraffe slightly reducing them (differences
263 between 1 and 3 individuals; Supplement Fig. S3 lists mean group sizes). As buffalo left the
264 study area, their mean group sizes also shrank drastically from hundreds to a dozen per
265 sighting (Supplement Fig. S3).

266 *The distance of species to the nearest water source*

267 The most parsimonious model (Table 2, full model 4) consisted of an interaction between
268 species identity, day (juldate) and transect classes (transect_GRR, river_class) and explained
269 variance fairly well (R^2 marginal effects = 0.73, R^2 conditional effects = 0.77 using the delta
270 method in R-package 'MuMIn', Barton 2022; Nakagawa et al. 2017). The model was not
271 overdispersed, although it still had heteroscedasticity in the residuals (diagnostic plot in
272 Supplement Fig. S4 a), and identified common duiker as an outlier with larger distances to
273 water than expected, and elephant, impala and zebra with shorter distances than expected
274 (Levene test for homogeneity of variance, diagnostic plot in Supplement Fig. S4 b).

275 Group sizes, i.e. size of species aggregations (species_count; additive effect) slightly
276 decreased with increasing distance from water (Supplement Table S1 and Fig. S5). Generally,
277 species had larger distances to water in perpendicular transects and the downstream transect,
278 and distances increased as the dry season progressed, except for buffalo which moved
279 upstream (Fig. 3). Maximum distances of > 12 km were mainly measured for common duiker
280 and impala.

281 Transect-ID still had an effect on distances to water beyond their description by fixed factors,
282 with transects 4 showing that species had closer distances to water than expected from
283 average, and at transect 8 they kept larger distances (Supplement Fig. S6). The closer
284 distances can be explained by transect 4 having a spring half way providing water (Fig. 1).
285 Both transects, 4 and 8, are very heterogeneous, contain a lot of vegetation and also predators
286 (Abade et al. 2014). However, we cannot rule out that the unexpected larger distances in
287 transect 8 as discovered by the random effect are an artefact of that transect not leading as
288 close to the GRR as the other alongside transects (Supplement Fig. S6).

289 In general, we could not discern any distance-to-water effects between species when they
290 were close to the main river (alongside GRR, Fig. 4) apart from buffalo that had a drastically
291 decreased distance to water in the downstream transect as they occurred closer to water in the
292 GRR. The effect of desiccation was exacerbated in the drier perpendicular transects. Here, of
293 the three grazers, buffalo and waterbuck maintained a shorter distance to water than any other
294 species (Fig. 4). In the upstream perpendicular transect, differences between the remaining
295 species (including greater kudu) did not exceed distances of approximately 1 km. Greater
296 kudu foraging in the midstream perpendicular transect were approximately 8 km away from
297 the nearest water source (Fig. 4). In the perpendicular downstream transect 5, we observed
298 stronger responses in terms of minimising distances to water for greater kudu, giraffe (both
299 browser) and elephant (mixed feeder) than in midstream transects, whereas the territorial

300 warthog and common duiker increased distances to water up to 13 km. In this extremely dry
301 area (perpendicular downstream), zebras, greater kudu and impala maintained similar
302 distances to the nearest source of water between 5 and 6.5 km at the start and at the end of the
303 dry season, respectively. Year of sampling did not play a role (Table 2; null model 2 with
304 largest delta AIC).

305

306 **Discussion**

307 Although national parks throughout Africa aim to protect wildlife from direct negative human
308 activities such as bushmeat hunting and livestock encroachment (Nyahono et al. 2005; Hofer
309 et al. 1996), wildlife within many African national parks is in decline because of human
310 activities indirectly impacting the parks (Ogutu and Owen-Smith 2003; Caro and Scholte
311 2007; Western, Russel and Cuthill 2009; Bartzke et al. 2018). Large scale water abstraction
312 from rivers upstream of national parks can substantially reduce the availability of surface
313 water to wildlife in protected areas during the dry season. Our findings reveal a range of
314 vulnerabilities of nine mammalian herbivores to the dry season loss of surface water from the
315 formerly perennial GRR within Ruaha NP. We report the effect of surface water availability
316 on the distribution of these herbivores within our study area between the early and late dry
317 season (Figs. 2 and 3) and the distance of these herbivores to the nearest source of surface
318 water. The measured distances to water were both a sign of water retracting due to drying up
319 as well as the reaction of species towards it, i.e. whether they relocate to the remaining areas
320 with water sources or cope with less access to water.

321 Transect counts provide an assessment of the relative importance of different locations in our
322 study site to the nine most common mammalian herbivores. Transects alongside the GRR
323 (Table 1, Fig. 2) held more animals per species for most (seven of the nine) species than the

324 perpendicular transects leading away from the GRR; the exceptions were common duiker and
325 warthog. It is likely that areas alongside the GRR contain more and/or better quality
326 resources (water, food and shade) required by most mammalian herbivores than those along
327 perpendicular transects. Animals in transects alongside the GRR were significantly closer to
328 surface water than those along perpendicular transects. This general effect depended on
329 species and transect type, with larger differences between transect type along downstream
330 transects, possibly because this section of the GRR regularly dried out in the past decades,
331 including the exceptionally wet El Niño year of 1993 (Mtahiko et al. 2006). As a result
332 ground water in this area may occur at a greater depth than when there was perennial flow in
333 this section of the river.

334 Consistent with previous studies (Western 1975; Thrasher et al. 1995; Redfern et al. 2003,
335 2005), we showed that the distribution of most African mammalian herbivores contracted
336 from the early to late dry season towards the section of the GRR with more surface water
337 (Fig. 3, Supplement Fig. S2). Typically, mammalian herbivores aggregate close to natural
338 sources of water or artificial waterholes. Our results illustrate the more general importance of
339 the GRR, including the downstream section that had dried-up by the late dry season. This
340 indicates that the GRR is not only important as a source of surface water, but also for other
341 resources and thus, as previously suggested, an essential component of the ecological health
342 of Ruaha NP (Epaphras et al. 2008; Stommel et al. 2016a,b; Roug et al. 2020). Only the
343 common duiker exhibited relatively limited contraction in its distribution in the late dry
344 season.

345 Of the nine species investigated, most animals were observed in areas close to the GRR
346 during the dry season (Table 1, Fig. 2), highlighting the importance of this river as a source of
347 water and other essential resources such as forage and shade. At the start of each dry season,
348 water flowed along the entire section of the GRR but by the late dry season large downstream

349 sections of the river were dry, with isolated water pools within the river bed (Stommel et al.
350 2016a). In addition, the downstream section is deeper (sea level) and hotter in contrast to the
351 upstream section, which might make a difference in thermoregulation for the big ones
352 (buffalo, elephant, giraffe). The few small scattered pools and waterholes dug by wildlife in
353 the downstream GRR river bed are important because no other surface water remained in this
354 section of the GRR approximately mid-way through the six month long dry season (Stommel
355 et al. 2016a). The presence of green forage growing within the dry downstream GRR riverbed
356 is an important food source for mammalian herbivores in this area. However, as the dry
357 season progresses, the ground water level probably sinks to a greater depth in the downstream
358 than upstream sections of the river. This may result in a faster decline in the nutritional
359 quality and water content of vegetation in the downstream leading to an earlier need to
360 increase water intake by herbivores in the downstream section due to the consumption of dry
361 forage (Owen-Smith 1990).

362 These changes most notably affected the distribution of one grazing species, the African
363 buffalo, which moved upstream out of the study area and national park (Figs. 2 and 3).
364 African buffalo, a highly water dependent species, were present in our study area during the
365 early dry season, when surface water was still available throughout most of the GRR
366 (Stommel et al. 2016a). Buffalo may remain close to water because they not only need to
367 drink frequently, but also because they can ruminate in water, lying in water or damp mud
368 may improve temperature regulation, and mud may deter ticks and biting flies (Prins and
369 Sinclair 2013). By the late dry season, the downstream stretch of the GRR had dried up,
370 which caused most buffalo to move out of our study area and upstream to the section of the
371 GRR that still contained surface water. Similarly, Roug et al. (2020) demonstrated that
372 buffalo in Ruaha NP during the dry season moved to stretches of the GRR that contained
373 surface water, and the loss of dry season surface water from the GRR was considered a factor

374 driving the decline in the buffalo population in Ruaha NP. As expected, waterbuck and
375 elephant also were close to water in all transects (Fig. 4).

376 Although elephants are mixed feeders, they require water for thermoregulation. Elephants
377 cool their large bodies by either submerging themselves in water or by spraying water over
378 their bodies. Elephants do not have sweat glands but as their skin's permeability increases
379 steadily as temperatures rise, body heat can be lost by cutaneous evaporative water loss, thus
380 elephants are termed obligate evaporative coolers (Dunkin et al. 2016). To maintain thermal
381 balance at high temperature, elephant have been estimated to use a substantial amounts of
382 water (22-100 l) within a period of 24 hr, depending of the ambient temperature (Dunkin et
383 al. 2016) and this indicates that regular access to water for thermal regulation is probably an
384 important factor determining the distribution of elephants (Chamaillé-James et al. 2007). The
385 ability of elephants to dig deep holes to access underground water in the dry GRR riverbed
386 during the dry season (Epaphras et al. 2008; Stommel et al. 2016a), is likely to become an
387 increasingly important adaptation for elephants in Ruaha NP if the offtake of water for crop
388 irrigation increases in future. Elephants also cool their bodies by increasing blood flow
389 through dermal capillaries in their large ears which they flap to shed and they can minimize
390 heat absorption by sheltering in shade (Dunkin et al. 2016).

391 Interestingly, our results indicate that the few giraffe sighted in the very dry perpendicular
392 downstream transect (Fig 1, transect 5) substantially reduced their distances to water,
393 indicating that they moved closer to remaining water pools in the area, which might have
394 been a wildlife dug water hole. Giraffe do drink, but their splayed leg stance is thought to
395 make them vulnerable to predation. This may suggest there is a threshold for this browser to
396 tolerate water scarcity or the pools are linked to another important resource such as high-
397 quality forage or shade. It is known that giraffe curtail time spent feeding to seek shade as
398 temperatures increase towards the middle of the day (du Toit and Yetman 2005).

399 The steepest dry season increase in the distance to the nearest surface water source was
400 apparent in common duiker and warthog (Fig. 4). This indicates that both remain within their
401 territories throughout the year, despite the increasing distance to surface water due to
402 desiccation during the late dry season. Within the spectrum of mammalian herbivores in this
403 study, common duiker and warthog are the species that are least dependent on surface water
404 and thus most resilient to the dry season decline in surface water availability.

405 The territorial common duiker has physiological and behavioural adaptations to dry
406 environments, and this species does not require the presence of surface water (Sutherland et
407 al. 2018; Bennet 2020), as its diet normally provides sufficient water (Wilson 2013). The
408 warthog is also a territorial species that requires underground burrows for breeding, shade
409 and the protection from predators (White 2010). Warthogs can vary their daily body
410 temperature by 7°C. The use of underground burrows probably helps to conserve energy and
411 reduce water loss when temperatures outside the burrow are high (Cummings 2013). Warthog
412 can access ground water by digging water holes (Epaphras et al. 2008; Stommel et al. 2016a).
413 These adaptations may explain the occurrence of warthogs in areas away from the GRR
414 throughout the dry season. Western (1975) described the warthog as water-bound, but we
415 found that the distance of warthogs from surface water along downstream perpendicular
416 transects was considerable, and this distance substantially increased during the dry season
417 (Fig. 4), i.e. warthog did not follow the progressing desiccation.

418 Greater kudu can survive without water if the food they consume contains sufficient moisture
419 (Owen-Smith 2013). In all transects alongside the GRR, kudu were relatively close to sources
420 of surface water throughout the dry season and their distance to water did not alter much as
421 the dry season progressed, even in the downstream transects where surface water was only
422 present in water pools and holes dug by wildlife, in the dry riverbed at the end of the dry
423 season. Along perpendicular transects, greater kudu had substantially larger distances to

424 surface water, but it is not known whether it was necessary for these animals to travel to
425 water sources to drink (Fig 4).

426 Although transects alongside the GRR suggest that impala prefer to remain relatively close to
427 sources of surface water throughout the dry season, impala in downstream perpendicular
428 transects maintained substantially larger distances from surface water (Fig 4). Plains zebra
429 also occurred relatively close to sources of surface water throughout the dry season in
430 upstream and midstream alongside transects, and at far larger distances from water sources in
431 perpendicular downstream transects. The ability of zebras to dig waterholes may allow zebras
432 to continue to use areas in Ruaha NP where poor water quality persists because reduced dry
433 season flow in the GRR might otherwise have limited their distribution.

434 Our results may underestimate the distance animals maintained to the sources of surface
435 water they used for drinking. Several species are known to dig holes to access underground
436 water, including elephants, plains zebra and warthog (Dudley et al. 2001; Epaphras et al.
437 2008), but waterholes dug by wildlife are thought to provide sufficient water for only a
438 limited number of large mammals and are insufficient for large herds of elephants or buffalo
439 (Owen-Smith 1996). Water holes dug by wildlife are abandoned when they become
440 contaminated with high bacterial loads, approximately 12 days after they were created
441 (Stommel et al. 2016a). We think the potential errors caused by the inclusion in our model of
442 abandoned waterholes that were no longer in use and the possible omission of a few water
443 holes used by wildlife for drinking is small. Once dug, water holes in Ruaha NP slowly fill
444 with sand and thus are typically used for a period of less than 14 days (Stommel et al. 2016b).

445 Dry season aggregations of mammalian herbivores near sources of surface water are known
446 to attract large carnivores (Hopcraft et al. 2005; Harrington et al. 1999; Davidson et al. 2013)
447 and are associated with seasonal changes in the distribution of lions and leopards in Ruaha

448 NP and surrounding protected areas (Abade et al. 2014). A high foraging success during the
449 dry season by large predators within Ruaha NP may explain the decline in cattle predation
450 from wet to dry season reported by households outside the park, at least those close to its
451 eastern boundary (Kalyahe et al. 2022). Large mammals are important species for tourism in
452 Ruaha NP, but there is growing evidence that the current loss of dry season flow in the
453 downstream section of the GRR is having a detrimental effect on water dependent large
454 mammals such as the hippopotamus and buffalo (Stommel et al. 2016b, Roug et al. 2020).

455 Even so, little is known about the likely long-term effect of the loss of dry season flow in the
456 GRR on the ecology of Ruaha NP and its high species diversity. In terms of its
457 biogeographical location, Ruaha NP lies at the transition between the East African *Acacia-*
458 *Commiphora* zone and the southern African *Brachystegia* miombo zone (Barnes 1983). The
459 documented upstream movement of hippopotamuses during the dry season is likely to
460 increase human-wildlife conflict in surrounding communities, when they have to search
461 outside the park for water or forage (Mtahiko et al. 2006). Furthermore, large-scale
462 movements of hippopotamuses upstream of the GRR can increase the spread of anthrax
463 (*Bacillus anthracis*) in Ruaha NP (Stears et al. 2021). Increased aggregation of animals
464 around diminishing sources of surface water as the GRR dries up during the dry season is
465 likely to increase the transmission of a range of pathogens (Huang et al. 2022).

466 In conclusion, the dietary niche of mammalian herbivores defines their general response to
467 human induced surface water scarcity in Ruaha National Park, Tanzania: Omnivores and
468 browsers are more resilient than mixed feeders and grazers, and this was modulated by
469 biophysical (thermoregulation in elephants) effects. Our results suggest that the African
470 buffalo is the most vulnerable species of the nine most important species considered to the
471 loss of water flow in the Great Ruaha River. Buffalo also are likely to suffer the largest
472 relative habitat loss of all species considered, comparable to the habitat loss already

473 documented in hippopotamuses (Stommel et al. 2016b). Overall, the results underline the
474 importance of dry season water resources in Ruaha NP, especially the water flow during the
475 dry season in the Great Ruaha River, to avoid dry season habitat loss for numerous species.
476 This involves a concerted action plan for sustainable agriculture outside the park to avoid
477 human-wildlife conflicts so that water irrigation does not come at cost for wildlife (Lemly et
478 al. 2000).

479

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702 **Table 1.** The total number of animals per species (sp) counted in five transects (tr) alongside (A) (transects 6-10 in Fig. 1) the GRR and
703 perpendicular (P) (transects 1-5 in Fig. 1) during early and late dry season (June-August; Sept –November) in 2011-2013. Total counts represent
704 the sum across the 11 sampling weeks per year and do not represent the true species abundances. Mean group sizes and mean distances to water
705 are averages across the sampling weeks. B: African buffalo, CD: common duiker, E: elephant, G: giraffe, I: impala, K: Greater kudu, Wb:
706 waterbuck, Wh: warthog, Z: zebra.

tr	sp	feed type	Total species count						Mean group sizes						Mean distances to water (m)					
			2011		2012		2013		2011		2012		2013		2011		2012		2013	
			early	late	early	late	early	late	early	late	early	late	early	late	early	late	early	late	early	late
A	B	grazer	1109	230	1178	102	182	95	138.6	46.0	107.1	51.0	22.8	15.8	343	714	287	248	429	414
A	E	mixed	141	146	109	137	172	258	5.6	5.2	5.5	5.3	6.9	6.3	457	830	508	698	622	656
A	G	browser	91	104	74	80	61	87	2.4	2.3	2.2	2.2	2.1	2.0	842	702	771	728	722	624
A	I	mixed	2967	2669	3332	3159	3663	3140	10.5	10.9	11.1	12.3	10.7	10.8	417	547	501	431	390	395
A	K	browser	52	96	61	111	43	127	4.3	4.6	5.1	4.8	3.9	4.4	753	575	940	436	712	510
A	Wb	grazer	40	21	21	16	12	36	2.9	3.5	2.6	2.3	3.0	4.5	584	886	479	672	475	560
A	Wh	omni	20	42	15	22	10	16	2.2	2.1	2.5	1.8	2.5	2.3	326	747	417	556	297	266
A	Z	grazer	48	82	151	211	57	149	8.0	5.5	8.9	8.4	7.1	7.8	871	758	720	602	659	676
A	CD	omni	NA	NA	NA	NA	NA	1	NA	NA	NA	NA	NA	1	NA	NA	NA	NA	NA	307
P	B	grazer	NA	2	2	NA	90	NA	NA	2	2	NA	90	NA	NA	669	1170	NA	2119	NA
P	E	omni	12	10	6	7	11	13	1.2	1.0	1.0	1.0	1.1	1.1	6129	7613	2517	7827	6253	7074
P	G	mixed	25	33	63	136	74	65	4.2	6.6	4.9	5.4	3.7	5.0	1577	1628	2772	2949	3038	2930
P	I	browser	90	55	92	56	69	45	2.3	1.8	2.2	1.5	2.2	1.9	2906	3650	3654	4777	3657	5131
P	K	mixed	618	617	698	863	755	531	7.4	8.0	5.6	7.6	6.7	4.8	3083	4950	3483	4384	3972	5652
P	Wb	browser	32	56	51	66	71	76	2.5	3.3	2.8	3.1	3.2	3.6	5127	5313	3839	6370	4486	6070
P	Wh	grazer	2	NA	NA	NA	NA	14	1.0	NA	NA	NA	NA	3.5	1417	NA	NA	NA	NA	2224
P	Z	omni	27	29	34	21	35	10	2.3	2.6	2.4	1.8	2.5	1.7	5857	3571	5251	6206	5877	9355
P	CD	grazer	86	102	91	33	58	51	6.1	6.4	5.4	4.1	5.3	3.9	2304	3516	3158	3034	2729	3256

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709 **Table 2.** Model selection table to assess the relative contribution of the progressing drying season (juldate; consecutive numbering of days since
 710 1st of June), the transect location (transect_GRR; alongside or perpendicular to Great Ruaha River), the direction of drying (river_class; transect
 711 location upstream, midstream or downstream) and group sizes (species_count; number of individuals in group of respective species) for the nine
 712 species on their distance to water (response variable). Transect-ID and year were taken as random effect. The best model is indicated in bold as
 713 assessed by the difference of the AIC values to the best model (delta AIC). df = degrees of freedom.

714

Model	Fixed effects (response = distance to water (m))	random effects	df	dAIC to best model
null model 1	~1	(1 year) + (1 transect_id)	4	272
null model 2	~1	(1 year)	3	5525.3
null model 3	~1	(1 transect_id)	3	270.1
full model 1	~ species * (juldate + transect_GRR + species_count)	(1 transect_id)	38	62.4
full model 2	~ species * (juldate + transect_GRR) + species_count	(1 transect_id)	30	50.9
full model 3	~ species * (juldate + transect_GRR)	(1 transect_id)	29	55.8
full model 4	~ species * (juldate + transect_GRR + river_class) + species_count	(1 transect_id)	48	0
full model 5	~ species * (juldate + transect_GRR + river_class + species_count)	(1 transect_id)	56	12.2
full model 6	~ species * (juldate + transect_GRR) + river_class	(1 transect_id)	31	55.6
full model 7	~ species * (juldate + transect_GRR) + river_class + species_count	(1 transect_id)	32	50.6
full model 8	~ species * (juldate + river_class) + species_count	(1 transect_id)	39	91.7

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717 **FIGURE LEGENDS**

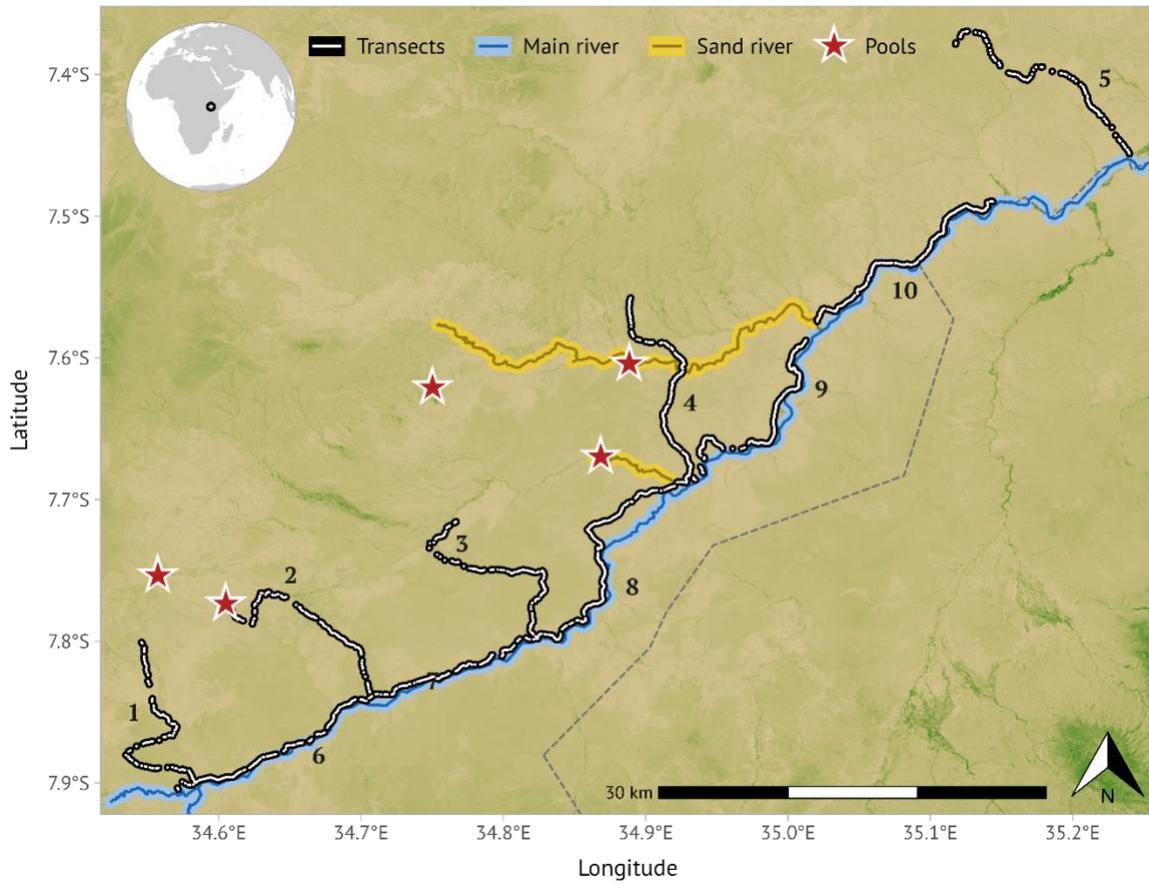
718 **Figure 1.** Map of the study area covering the east of Ruaha National Park in central
719 Tanzania. Ground transects were located in northwesterly direction either leading away from
720 the GRR, the “perpendicular transects” 1-5, or along the GRR, the “GRR transects” 6-10.
721 Stars: Permanent non-GRR locations with surface water (springs) during all years of the
722 study period and during the whole time of dry season (modified after Stommel et al. 2016a).
723 Mkwawa spring (located at the end of transect 2) was only water-filled in 2011. The colour
724 code is the normalized difference vegetation index NDVI in logarithmic scale for July 2011
725 (LandSat 8); the greener, the higher the productivity of the vegetation. The NDVI geodata
726 were provided by the US Geological Survey (<https://www.usgs.gov/landsat-missions/landsat-normalized-difference-vegetation-index>). Thin grey line: park border.

728 **Figure 2.** Species count across years per study site compartment and dry season in increasing
729 desiccation from left to right: upstream-alongside (U-A, transects 6 and 7), upstream-
730 perpendicular (U-P, transects 1-3), midstream-alongside (M-A, transects 8 and 9), midstream-
731 perpendicular (M-P, transect 4), downstream-alongside (D-A, transect 10) and downstream-
732 perpendicular (D-P, transect 10) (Fig. 1). Please note that the y-axis is different for each
733 species. The figures represent the sum of species seen each sampling week and do not
734 represent true abundances.

735 **Figure 3.** The density distribution of zebra, waterbuck and buffalo during the (a) early (June-
736 August, 6 sampling events) and (b) late dry season (September-November, 5 sampling
737 events), summarised across all three dry seasons from 2011 to 2013. The density distribution
738 was weighted according to the number of individuals observed.

739 **Figure 4.** The effect plots for each species, showing the predicted distance to the nearest
740 surface water as a function of dry season date with day 1 set as the 1st June in interaction
741 with transect characteristics (alongside-perpendicular or up-mid-downstream). Filled area:
742 the 95% confidence interval around the estimated regression line.

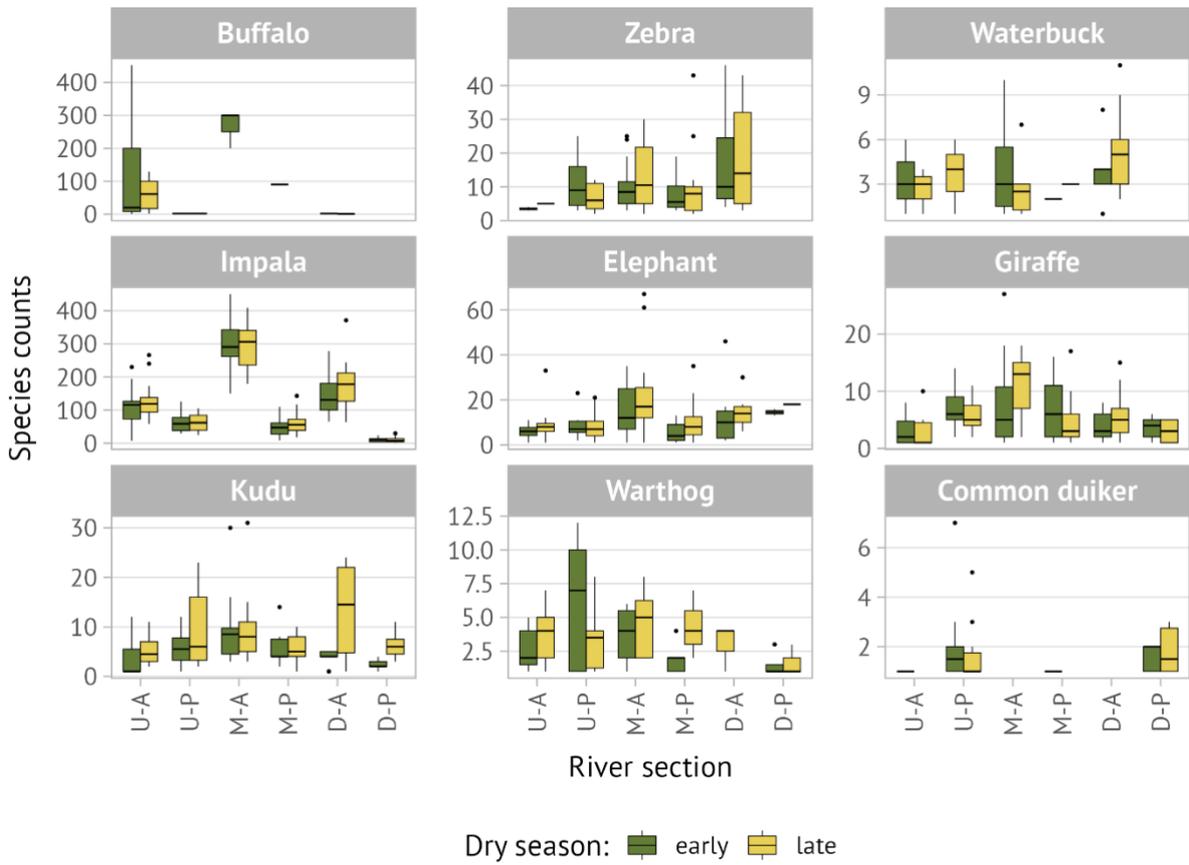
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746 Figure 1

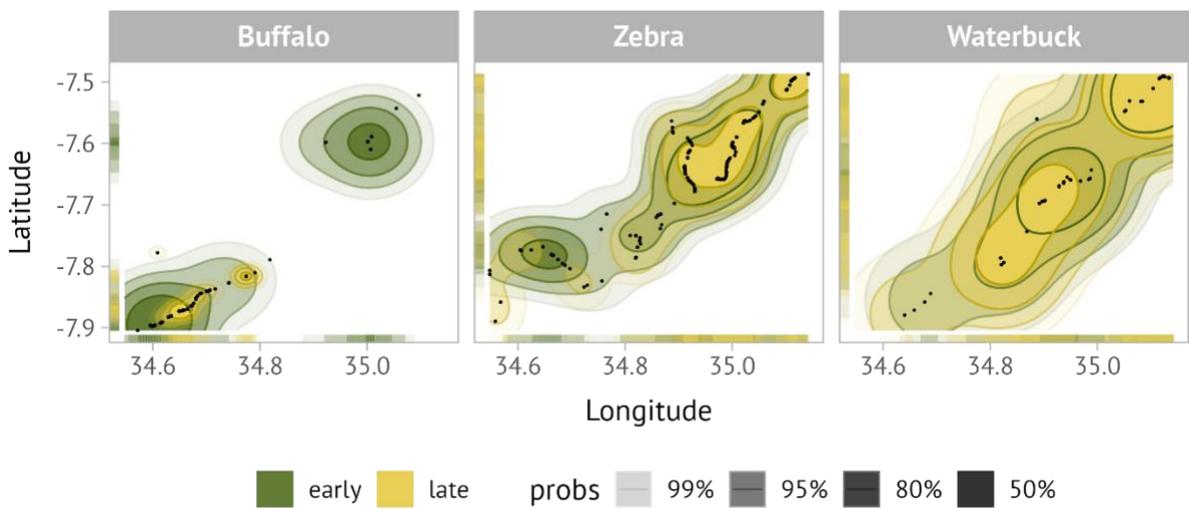
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749 Figure 2

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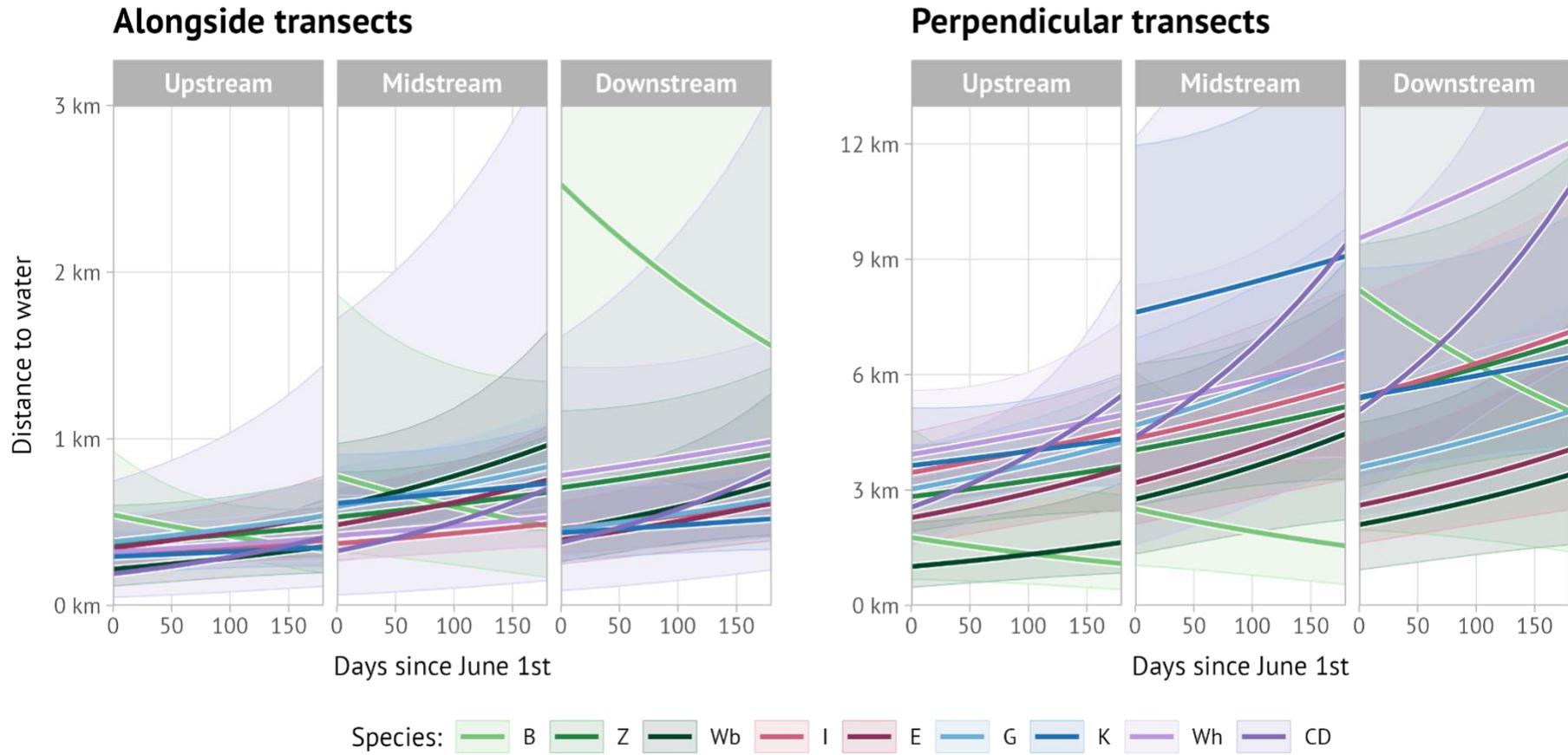


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752 Figure 3

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757 Figure 4

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