

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

Abstract

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

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

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

Introduction

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

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

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

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

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

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

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

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

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

Methods

Study site

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

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

Data collection and study species

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

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

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

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

Dietary categories of herbivores

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

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

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

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

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

Statistical analysis

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

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

Results

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

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

The distance of species to the nearest water source

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

NP and surrounding protected areas (Abade et al. 2014). A high foraging success during the dry season by large predators within Ruaha NP may explain the decline in cattle predation from wet to dry season reported by households outside the park, at least those close to its eastern boundary (Kalyahe et al. 2022). Large mammals are important species for tourism in Ruaha NP, but there is growing evidence that the current loss of dry season flow in the downstream section of the GRR is having a detrimental effect on water dependent large mammals such as the hippopotamus and buffalo (Stommel et al. 2016b, Roug et al. 2020). Even so, little is known about the likely long-term effect of the loss of dry season flow in the GRR on the ecology of Ruaha NP and its high species diversity. In terms of its biogeographical location, Ruaha NP lies at the transition between the East African *Acacia-Commiphora* zone and the southern African *Brachystegia* miombo zone (Barnes 1983). The documented upstream movement of hippopotamuses during the dry season is likely to increase human-wildlife conflict in surrounding communities, when they have to search outside the park for water or forage (Mtahiko et al. 2006). Furthermore, large-scale movements of hippopotamuses upstream of the GRR can increase the spread of anthrax (*Bacillus anthracis*) in Ruaha NP (Stears et al. 2021). Increased aggregation of animals around diminishing sources of surface water as the GRR dries up during the dry season is likely to increase the transmission of a range of pathogens (Huang et al. 2022).

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

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

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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 perpendicular (P) (transects 1-5 in Fig. 1) during early and late dry season (June-August; Sept –November) in 2011-2013. Total counts represent 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 are averages across the sampling weeks. B: African buffalo, CD: common duiker, E: elephant, G: giraffe, I: impala, K: Greater kudu, Wb: 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 |

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.

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| 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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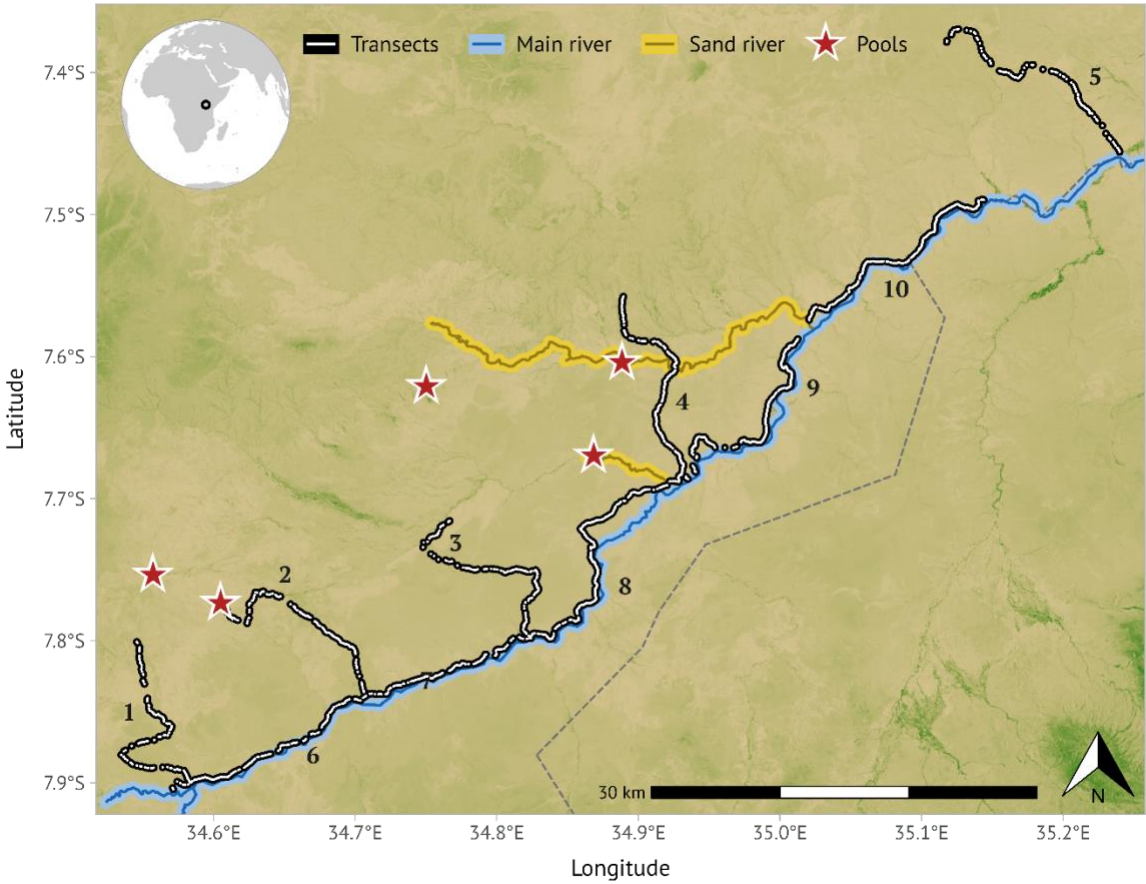
FIGURE LEGENDS

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

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

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

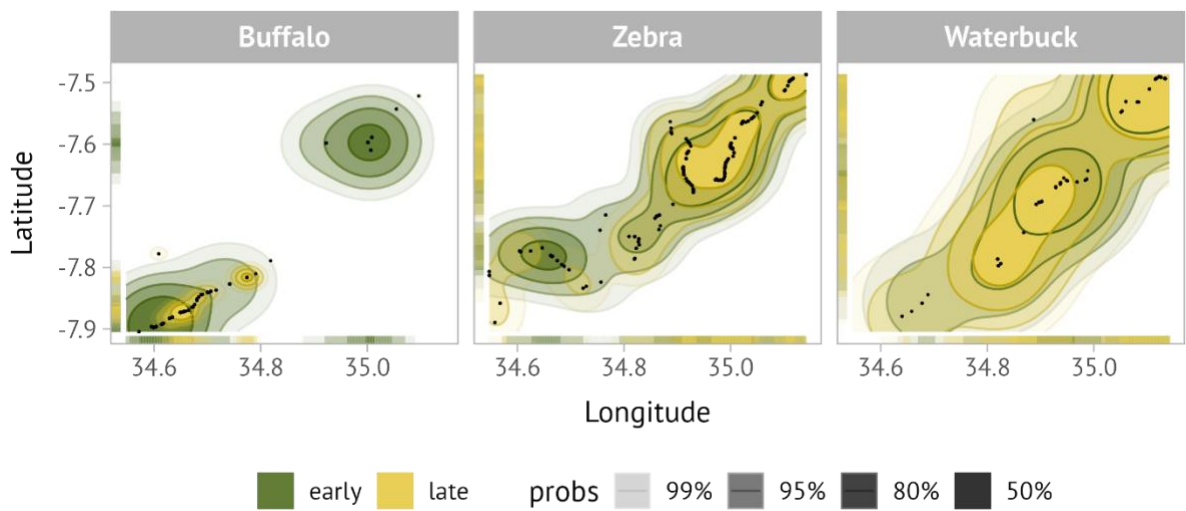
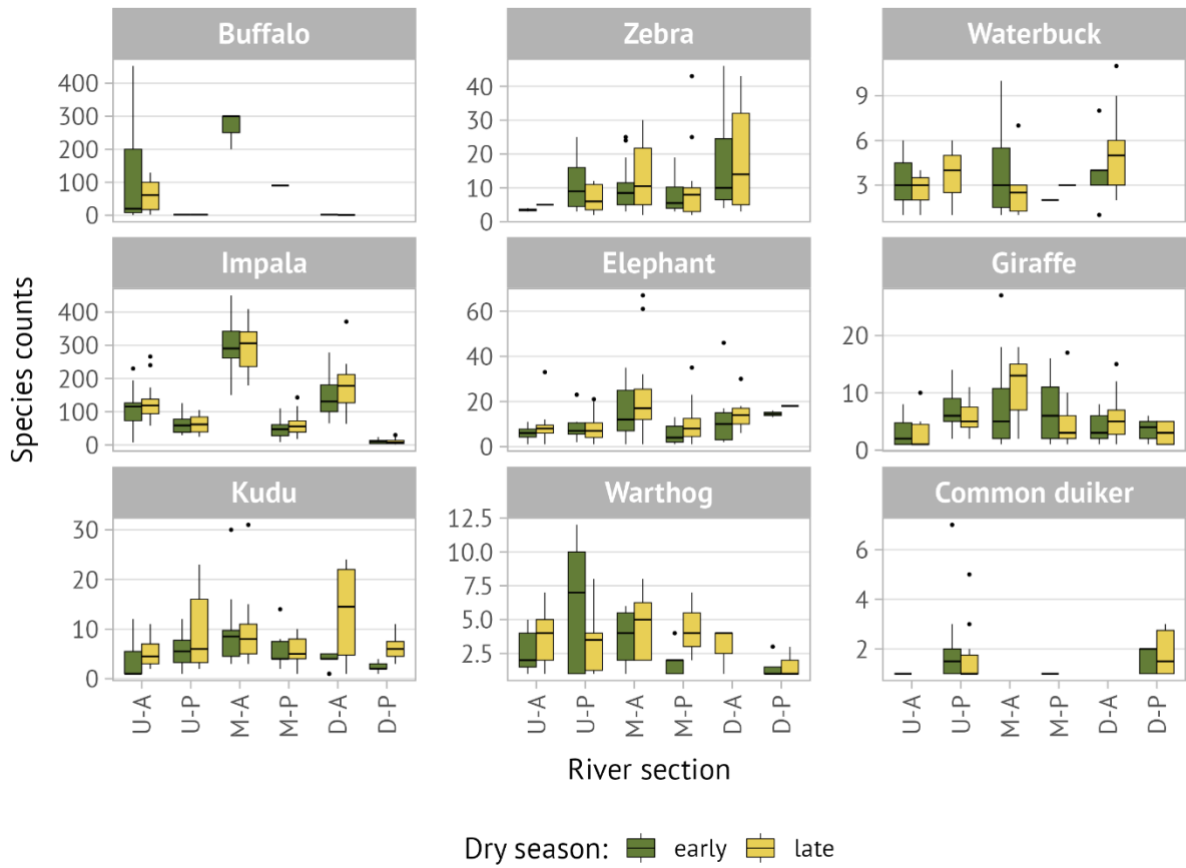
Figure 4. The effect plots for each species, showing the predicted distance to the nearest surface water as a function of dry season date with day 1 set as the 1st June in interaction with transect characteristics (alongside-perpendicular or up-mid-downstream). Filled area: the 95% confidence interval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



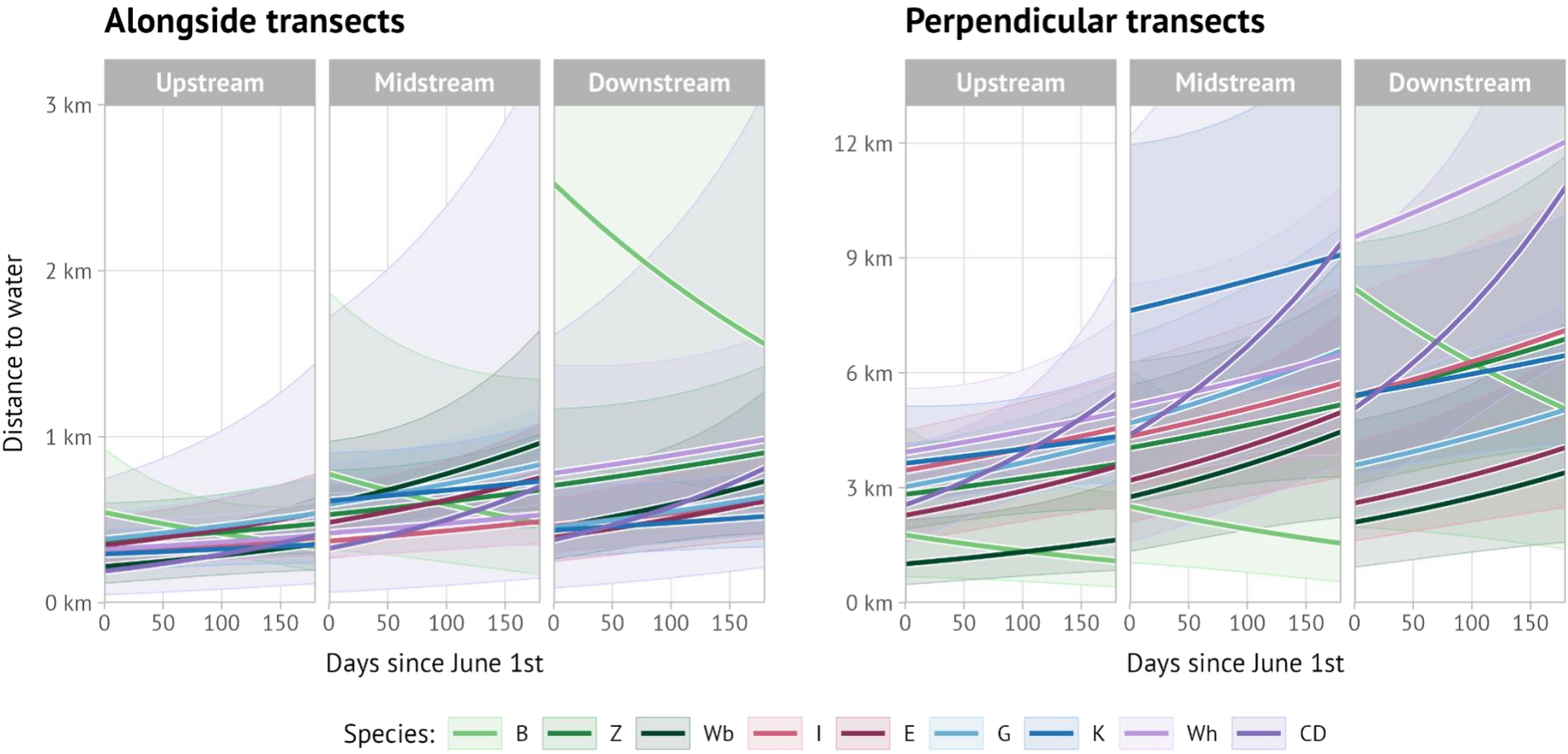
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746 Figure 1

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757 Figure 4

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