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Research article

Effect of human induced surface water scarcity on herbivore distribution during the dry season in Ruaha National Park, Tanzania

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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 (Ruaha NP) in southern Tanzania, one of the largest parks in Africa, contains important wildlife populations, including rare and endangered species. The Great Ruaha River (GRR) 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 out during the dry season. The dry season distribution of a species in relation to surface water is considered an indicator of its dependence on water and ability to cope with the loss of surface water. We investigated how diminishing surface water availability during three dry seasons (2011–2013) affected herbivores' distance to water in Ruaha NP. The distance held by herbivores to water is shaped by a range of factors including dietary category. We determined changes in the locations of available surface water throughout the dry season using standardized ground transects, close to and leading away from the GRR, to map the locations of nine herbivore species. Functional responses of herbivores, i.e. their change in distance to water between early and late dry season, indicated that distance to water was 1) shortest in buffalo and waterbuck (grazers), 2) similar for plains zebra (grazer), elephant and impala (mixed feeders), 3) larger in giraffe and greater kudu (browsers) and 4) largest in generalist feeders (warthog, common duiker). The substantial species' differences in surface water dependence broadly fit predicted species differences in their ability to cope with anthropogenic reduction in surface water in Ruaha NP.

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

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Introduction

Surface water is utilised by humans for many purposes, including crop irrigation, livestock production, electricity generation and domestic use (Lemly et al 2000, Malmqvist and Rundle 2002, Dudgeon et al. 2006) and this can have negative ecological effects on ecosystems both locally and on a larger scale (Pringle 2001, Higgisson et al. 2020). 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 (Rockström and Falkenmark 2015, Johansson et al. 2016, Ogutu et al. 2016).

Human activities both within and outside protected areas in Africa 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). The construction of more than 300 artificial permanent water sources further altered animal distribution in the Park (Pringle 2001, Redfern et al. 2003, Smit et al. 2007).

Surface water is lost by evaporation during African dry seasons as there is little or no rainfall for several months. As ephemeral sources of surface water dry out, the locations where surface water occurs diminish as the dry season progresses (Redfern et al. 2005, Stommel et al. 2016a). In response, water dependent herbivores alter their distribution throughout the dry season to locations near remaining sources of surface waters. In protected areas with permanent sources of surface water, such as the perennial rivers in the north of the Serengeti ecosystem (Norton-Griffiths et al. 1975), and/or permanent artificial water holes, water dependent herbivores have been reported to aggregate near these permanent water sources as ephemeral sources dry out during the dry season (Western 1975, Thrash et al. 1995, Owen-Smith 1996, Redfern et al. 2003, Chamaillé-Jammes et al. 2007, Veldhuis et al. 2019). In Ruaha NP in central Tanzania, common hippopotamus *Hippopotamus amphibius* (hereafter hippopotamus) aggregate in large numbers during the dry season in upstream locations of the Great Ruaha River (GRR) that retain running water (Stommel et al. 2016b) and satellite-collars on 12 female African buffalo *Syncerus caffer* also indicate movement upstream to areas of the GRR with flowing water (Roug et al. 2020). Generally, the response of herbivores in Ruaha NP to changes in the availability of surface water in the dry season has not been investigated.

The distance herbivore species range from surface water during the dry season provides a general measure of their dependence on water. This is shaped by species specific factors such as diet, digestive physiology, temperature regulation mechanisms, body size and adaptations to limit 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). The distribution and abundance of food and predators may also play a role (Veldhuis et al. 2019). 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, Kay 1997). This suggests that the distance of grazers such as buffalo, plains zebra *Equus quagga* (hereafter zebra), and waterbuck *Kobus ellipsiprymnus* to surface water should be less than that of mixed-feeders such as African elephant *Loxodonta africana* (hereafter elephant) and impala *Aepyceros melampus*, and browsers such as giraffe *Giraffa camelopardalis* and greater kudu *Strepsiceros zambesiensis* (hereafter kudu). Generalist feeders such as warthog *Phacochoerus africanus* and common duiker *Sylvicapra grimmia* (hereafter duiker) that consume underground plant structures such as tubers, rhizomes, fruits and animals (e.g. insects, reptiles, small birds and mammals) that contain more water than plant matter grazed or browsed in the dry season should be less dependent on surface water than either grazers or browsers.

In addition to dietary category, digestive physiology and thermoregulation may affect a species' dependence on water. Hindgut fermenters, such as zebra, elephant and warthog produce more moist faeces than ruminants, thus may require more water than similar sized ruminants (Cain et al. 2012). Waterbuck 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 adapted to arid environments such as the common duiker that rarely need to drink, produces concentrate urine and dry faeces, and tolerates a far larger variation in body temperature before temperature regulation mechanisms are required (Wilson 2013, Sutherland et al. 2018, Bennitt 2020). Greater kudu can also exist for considerable periods without drinking provided the forage they browse contains sufficient water. In the dry season this may not be the case, particularly when precipitation at the end of the wet season is low (Owen-Smith 1990). Giraffe drink water but are relatively independent of surface water as they are thought to obtain their water requirement mostly from plants and dew (Redfern et al. 2003, Ciofolo and Le Pendu 2013).

Surface water is crucial for thermoregulation, particularly in some large bodied species such as buffalo (Prins and Sinclair 2013) and elephant (Dunkin et al. 2016) and also to prevent sun damage to the skin of hippopotamus (Eltringham 1993). Buffalos wallow or lie in water to shed heat and for this they require sources of surface water large enough to accommodate their body. By contrast elephants can cool their bodies by extracting water from relatively small self-dug water holes (Stommel et al. 2016a) with their trunk to spray water over their body. These differences in surface water requirements may affect the dry season distribution of buffalo and elephant.

We use the spatial distribution of species and their distance to the nearest surface water as an indicator of their likely vulnerability to future climatic events such as prolonged dry seasons, droughts and reductions in surface water availability due to excess water abstraction from perennial rivers. The main source of surface water for wildlife in Ruaha National Park (Ruaha NP), in central Tanzania, is the Great Ruaha River (GRR) (Mtahiko et al. 2006). Large scale abstraction of water from this river for irrigation upstream of Ruaha NP is considered responsible for the substantial decline in dry season flow since the early 1990s, and the drying out of large sections of this formerly perennial river within the Ruaha NP during the dry season (Mtahiko et al. 2006). This dry season decline in flow 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-out of large sections of the GRR substantially alters the distribution of the populations of hippopotamus (Stommel et al. 2016b) and African buffalo (Roug et al. 2020) in Ruaha NP. Currently, little is known about the impact of water abstraction from the GRR on other wildlife species 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.

In June, at the start of the dry season, the entire course of the GRR within Ruaha NP contains flowing water, and surface water also occurs in many rain filled depressions, in discrete pools in the riverbed of ephemeral tributaries, natural springs and natural wildlife dug water holes. Rain-filled depressions dry out quickly in the early dry season, and flow in the downstream part of the GRR stops by about the end of August, which results in a significant decline in water quality (Stommel 2016a). By October most of the downstream section of the GRR in Ruaha NP is dry, apart from a few pools (Mtahiko et al. 2006, Stommel 2016a). These losses of surface water lead to a continual loss of locations where herbivores can drink, and in response water dependent herbivores need to continually shift their distribution to remain in the vicinity of a source of surface water.

We investigated the extent to which dietary category, digestive physiology and mechanisms (behavioural and physiological) to prevent water loss affected the distance nine species maintained to the nearest source of surface water throughout the dry season. We expected 1) grazers to maintain shorter distances to surface water than browsers and mixed-feeders, and 2) species lacking physiological and/or behavioural adaptations to prevent water loss to remain closer to sources of surface water than species with these adaptations. To test these predictions we measured the location of individuals in each nine species sighted within 100 m each side of the same survey routes throughout the dry season. We also used this measure as a possible index of species vulnerability to future reduction of surface water availability in Ruaha NP, given that water abstraction is likely to increase with human population growth (Roberts 2011), and/or annual precipitation

may decline as some climate change scenarios for East Africa predict (Chen and Georgakakos 2015, Rowell et al. 2015).

Material and methods

Study site

The study was conducted during three dry seasons (2011–2013) within Ruaha NP in central Tanzania, which is located at the transition between the East African *Acacia–Commiphora* zone and the southern African *Brachystegia* miombo zone (Barnes 1983). Ruaha NP was established in 1964 and was expanded in 2008 to include the Usangu Game Reserve, making it one of the largest (20 226 km^2) national parks in Africa (Mtahiko et al. 2006). The Eastern Usangu wetland is an important source of water for the GRR and biodiversity hotspot. Before this, encroachment by livestock reduced water retention in the Eastern Usangu wetlands. Until the early 1990s, there was running water throughout the year in the section of the GRR through Ruaha NP and associated protected areas, except for a brief period in 1954. By 1993, the GRR was an ephemeral river chiefly due to large scale water abstraction for rice production upstream of Ruaha NP (Mtahiko et al. 2006). Prior to the loss of seasonal flow from the GRR a few aerial surveys of the distribution of elephants and other large herbivores in Ruaha NP were conducted and aggregated results were presented for large zones within the park (Norton-Griffith 1975, Barnes and Douglas-Hamilton 1982). The considerable differences in survey methods and the aggregation of results across large areas prevents meaningful comparison between our findings with these earlier studies.

The study area (Fig. 1) is described in detail by Stommel et al. (2016a). The spatial and temporal distribution of surface water during the dry season for each year of the study are provided by Stommel et al. (2016a,b). In brief, in the three years of the study (2011–2013) at the beginning of each dry season in June, the entire course of the GRR within the study area, including the section with alongside transects, contained flowing water. In June, surface water in the form of pools and wildlife dug water holes occurred at discrete locations in ephemeral sand river tributaries of the GRR including those with perpendicular transects, and natural springs (Fig. 1). Some locations in ephemeral rivers and springs in the study area retained water throughout one or more dry seasons (Stommel 2016a, b). In all years of the study, surface 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. By October, in all three years, most of the downstream section of the GRR was dry, apart from a few pools (Fig. 1). All rain-filled depressions in the study area dried out soon after the start of the dry season (Stommel 2016a).

Data collection and study species

Counts of individuals of each species sighted along 10 ground transects that used an existing game viewing tract were
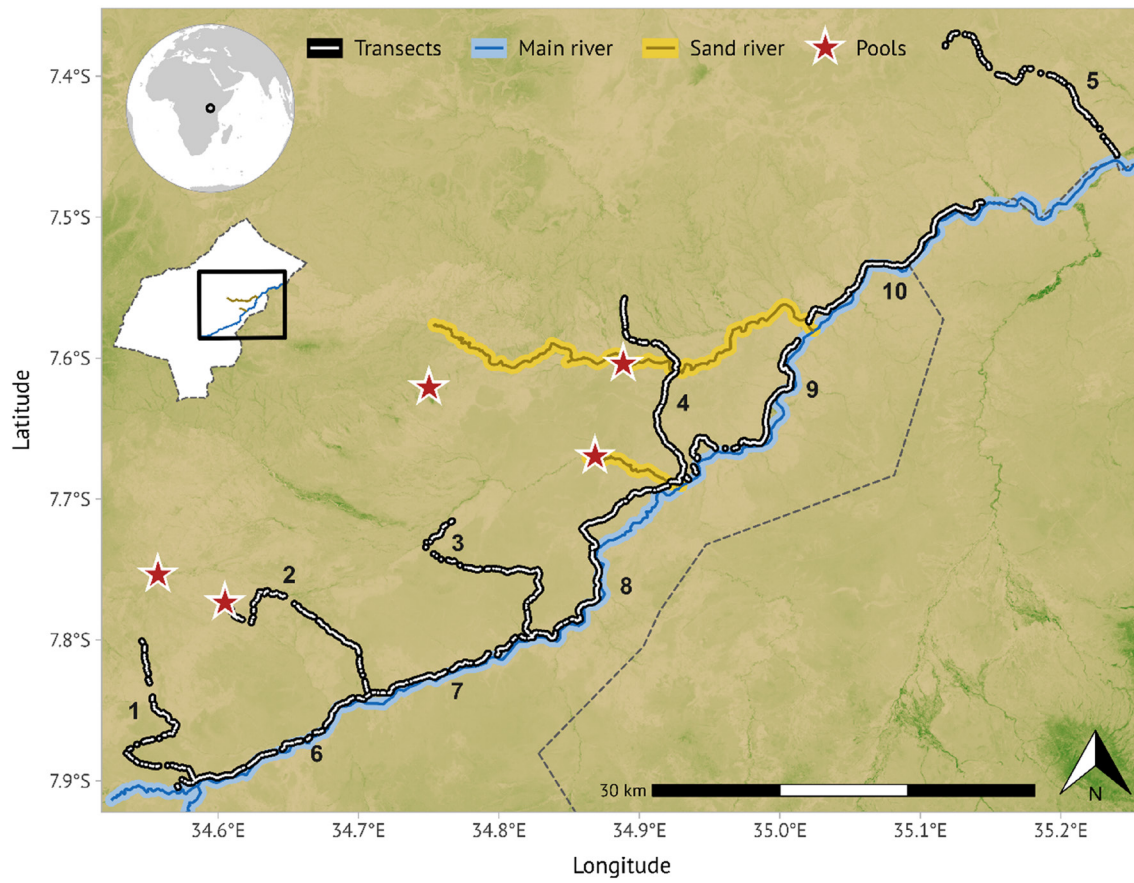
Figure 1. Map of the study area in the southeast of Ruaha National Park in East Africa. The location of 10 ground transects is shown including five perpendicular transects (P1–P5) leading away from the Great Ruaha River (GRR) and five transects alongside the GRR (transects A6–A10). Stars: Most springs provided surface water throughout the three dry seasons of the 2011–2013 period, except Mkwawa spring near transect P2 that was dry in 2012 and 2013 (modified from Stommel et al. 2016a). 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 (www.usgs.gov/landsat-missions/landsat-normalized-difference-vegetation-index). Thin grey line: park border.

conducted at intervals of approximately 14 days from June to October and once in November during the dry seasons of 2011, 2012 and 2013; thus each transect was surveyed 11 times per year (Fig. 1). To visualize how the progress of the dry season was associated with changes in the distribution of species in the study area, transect data were divided into early (June–August, each transect surveyed six times) and late dry season (September–November, each transect surveyed five times). Transects were approximately 20 km (mean transect length 19 880 m ± 115.3 m [standard error of mean, SEM]) in length. Five transects were alongside the GRR (A transects 6, 7, 8, 9 and 10), and five transects lead away from the GRR perpendicular to the course of the river (P transects 1, 2, 3, 4 and 5, Fig. 1). This resulted in two transect categories ('alongside', 'perpendicular') that differed in their distance to the GRR, vegetation type and water availability at the start of the dry season. Hence, the main differences between transects influencing detectability of species are encapsulated in these two categories, whereas available surface water is a variable that changed during the dry season and was updated at each survey.

To investigate the effect of the availability of surface water on herbivore distribution, we recorded as dynamic variables the locations of species sightings and their counts and the locations of available water surface in the following way: Data along transects were collected between 7:00 and 11:00 h in the morning. Sightings of the nine most numerous herbivore species were recorded, including buffalo, waterbuck, zebra, giraffe, kudu, impala, elephant, warthog and common duiker. For each sighting, we also recorded species counts, i.e. the number of individuals of a species per sighting (group sizes), to account for large aggregations in areas containing larger sources of surface water. We did not include the hippopotamus because this species' dependence on surface water in Ruaha NP is reported elsewhere (Stommel et al. 2016b). We restricted our sightings to animals within 100 m of the survey vehicle to maximize detection and assumed equal bias in detection across the study area. We could not formally account for imperfect detection and hence animals that potentially were missed, but we assume any bias to be similar in the two transect categories. For each sighting of

an animal or a group of animals, the perpendicular distance between the animal sighting to the transect line was measured with a laser range finder (Bushnell, PinSeeker 1500 7 × 26). However, only the GPS coordinates (latitude, longitude) of the locations of each animal or group were taken when animals were first sighted to minimize possible error due to animals shifting position in response to an approaching vehicle. Thus locations were not routinely taken when animals were perpendicular to the vehicle, neither was perpendicular distance recorded. As the maximum distance for recording any animal to the right and left of the vehicle along all transects was set at 100 m, this method resulted in a maximum bias of ± 100 m for locations.

The location of all available sources of surface water in the study area was also monitored from the beginning to the end of the dry season as detailed by Stommel et al. (2016a). That is, while driving along each transect, not only species identity and group size was recorded, but also the GPS location (latitude, longitude) of available water sources. We cannot exclude the possibility that we may have missed some small, ephemeral water sources such as small wildlife-dug waterholes, but we do not think we missed any major sources of surface water as these are well known to rangers in the dry season.

To analyse whether herbivores change their location in relation to the location of surface water, which shifts spatially during the course of the dry season due to evaporation and the digging of water holes by wildlife, we calculated the Euclidean distances (m) from the species' GPS location to the GPS location of the nearest surface water in the respective sampling week. Please note that both, species location and the position of surface water, can shift from one sampling period to the next, as the pools and water courses dry out. To calculate the nearest distance between species coordinates and water coordinates, we used the statistical software package R, ver. 4.2.1 (www.r-project.org) and the function *dist* for matrix calculations and selected the minimum distance to any water location for a respective species location.

Dietary categories of herbivores

The diet of African herbivores has been categorised using 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. This particularly applies to mixed-feeders such as impala that change from predominantly grazing grass during wet periods to browsing during dry periods (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 at the start of the dry season. Even so, we recognise that dietary categories occur along a continuum and a species category might change with habitat and during the course of dry season.

African buffalos are typically considered grazers of grasses and sedges even though they occasionally browse (Prins and Sinclair 2013). Waterbuck are considered grazers because their diet is dominated by grass (Cerling et al. 2003, Sponheimer et al. 2003), although they may also browse in the late dry season or early wet season (Spinage 2013). Grass dominates the diet of plains zebra, thus zebras are considered grazers (Duncan et al. 1990). Giraffe are considered 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 (Ciofolo and Le Pendu 2013). Greater kudus are typically classed as browsers as 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 a high ratio of protein to fibre, and also consume woody vegetation and the leaves and bark of certain tree species (Poole et al. 2013).

A stable isotope study categorised warthogs as hyper-grazers (Harris and Cerling 2002), but although the wet season diet is mostly grass, the dry season diet is broad and includes rhizomes, fruits, tree pods, tubers, bulbs, carrion and the predation of small mammals (Radke 1985, Blair 2012, Cumming 2013). Following Kihwele et al. (2020) we classified warthogs as generalist feeders during the dry season. As the diet of the common duiker consists of browse, fruits, flowers, fallen leaves, small herbs, seeds, insects, lizards, carrion and young birds (Wilson 2013) we classified common duikers as generalist feeders. In summary, we categorise African buffalo, waterbuck and plains zebra as predominantly grazers, giraffe and greater kudu as predominantly browsers, impala and elephant as mixed feeders whose diet shifts to browsing in the dry season and warthog and common duiker as generalists in the Ruaha NP dry season.

Statistical analysis

The following analyses were conducted using R ver. 4.2.1 (www.r-project.org). We used a generalised linear mixed-effects model framework (GLMM; Zuur et al. 2009) to investigate factors that best explained the distance of species to the nearest source of surface water (variable name: distance to water; response variable). Predictors included species identity (species) and day of the dry season calculated from the start of the dry season set to 1 June (juldate). Transects were classified as either perpendicular or leading alongside the GRR (transect_GRR). We included for each sighting of a species the number of individuals in each group sighted (species_count) as well as the dietary category of each species (diet_cat). Year and transect-ID were included as random effects to account for variance between years or transects that cannot be captured by fixed 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 2016) 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 (Supporting information). To avoid overdispersion, we fitted negative binomial models using the function *nbinom2* in the R package 'glmmTMB' (www.r-project.org, Brooks et al. 2017, VerHoef and Boveng 2007). We tested several models with increasing complexity, i.e. considered the above mentioned variables additively or in interaction with species identity and/ or dietary category, and used AIC to rank the models. We checked the explanatory power (R^2) of the model using the delta method in R-package 'MuMIn' (www.r-project.org, Nakagawa et al. 2017, Barton 2022). We selected the final model based on parsimony (i.e. lowest number of parameters) that were in the range of statistical support (delta AIC < 7; Burnham et al. 2011) and used the R package 'DHARMa' for model diagnostics (www.r-project.org, Hartig 2022).

Results

Species distribution

In general, species sightings and counts increased for zebra, giraffe, elephant, warthog and kudu especially in transects leading parallel to the main river course ('alongside'

transects) in the dry season, whereas they decreased for giraffe and warthog in the perpendicular transects (Fig. 2, Table 1, Supporting information). Practically all common duiker and most warthog (both generalist feeders) were sighted on perpendicular transects (Fig. 2). Most impala and elephant (both mixed feeders) were sighted in 'alongside' transects (Fig. 2), with fewer elephants present in the early than late dry season, whereas impalas were sighted in similar numbers in the early and late dry season. Buffalo (grazer) counts on 'alongside' transects were much higher in the early dry season (Fig. 2) when water flowed in the entire section of the GRR within the study site than in the late dry season when water was only present in the upper river section around transects 1 and 6. Buffalo numbers collapsed during the late dry season, with most remaining buffalo confined to the 'upper' section of the GRR (visualised in Supporting information). Most zebra were counted on transect in the 'alongside' section of the GRR that contained flowing water only in the early dry season (Fig. 2, Supporting information). Similarly, counts of kudu and giraffe (both grazers) were also most numerous at the 'alongside' section, particularly in the late dry season (Fig. 2, Supporting information). Counts of waterbuck (grazer) were low throughout the dry season. In general, buffalo and impala counts were much higher than the counts of other species, and common duiker sightings were rare. Group sizes (counts of individuals of the same species per sighting), differed only slightly between the 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;
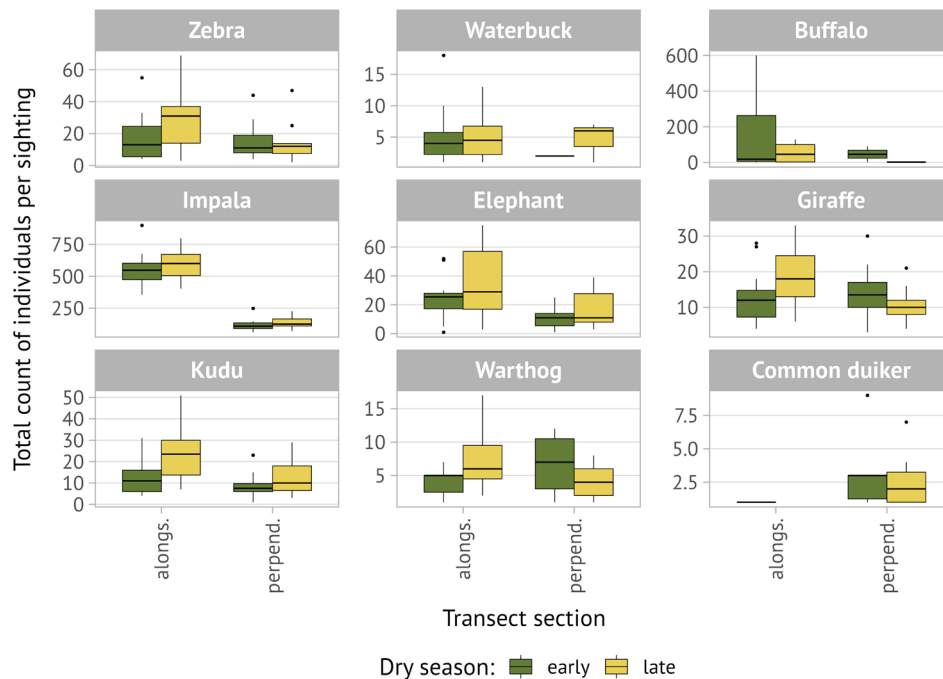
Figure 2. Total species count across years per transect class (alongside, perpendicular) and dry season period (early and late) (Fig. 1). Please note that the y-axis is different for each species. The figures represent the sum of species seen at each transect drive (bi-monthly) and do not represent true abundances, because we did not account for imperfect detection.

Table 1. The total number of animals per species (sp) counted in five transects (tr) alongside (A) (transects 6–10 in Fig. 1) the Great Ruaha River and perpendicular (P) (transects 1–5 in Fig. 1) to this river in Ruaha National Park during early and late dry season (June–August; September–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. Buffalo: African buffalo, Com dk: common duiker, Elephant: African elephant, Gt Kudu: Greater kudu, Wbuck: waterbuck, Wh: warthog, Zebra: Plains zebra. Number of sighting events per species, season and transect category are summarised in the Supporting information.

Tr	Species	Diet Cat	Total species count						Mean group size						Mean distance 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	Buffalo	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	Elephant	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	Giraffe	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	Impala	Mixed	2969	2669	3332	3159	3663	3140	10.5	10.9	11.1	12.3	10.7	10.8	417	547	501	431	390	395
A	Gt kudu	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	Wbuck	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	Warthog	Generalist	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	Zebra	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	Com dk	Generalist	NA	NA	NA	NA	NA	1	NA	2	NA	NA	NA	1.0	NA	NA	NA	NA	NA	307
P	Buffalo	Grazer	NA	2	2	NA	90	NA	NA	2	2	NA	90	NA	NA	669	1170	NA	2119	NA
P	Elephant	Mixed	25	33	63	136	74	56	4.2	6.6	4.9	5.4	3.7	5.0	1577	1628	2772	2949	3038	2930
P	Giraffe	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	Impala	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	Gt kudu	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	Wbuck	Grazer	2	NA	NA	NA	NA	14	1.0	NA	NA	NA	NA	3.5	1417	NA	NA	NA	NA	2224
P	Warthog	Generalist	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	Zebra	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
P	Com dk	Generalist	12	10	6	7	11	13	1.2	1.0	1.0	1.0	1.1	1.1	6129	7613	2517	7827	6253	7074

Supporting information lists mean group sizes). The mean group size for buffalo also shrank drastically from hundreds to a dozen per sighting (Supporting information). Total species counts, mean group size and mean distance to the nearest source of surface water for nine herbivores species in the early and late dry season of the years 2011–2013 are presented in Table 1. Total counts for each species in the early and late dry season are plotted in Fig. 2, numbers of sightings are provided in the Supporting information, and median distances to water of each species in Fig. 3.

The distance of species to the nearest water source

In general, during the course of the dry season most species shifted their location close to water pools in the alongside transects (Fig. 3 left panel). However, in the perpendicular transects, the distance to water for impala, kudu, warthog and duiker increased in comparison to the early dry season. This suggests that as sources of surface water dried up these species did not move closer to those water sources that were still available. In contrast to these species, grazers like waterbuck and buffalo had the shortest distances to water along perpendicular transects or were absent (Fig. 3 right panel). Grazers either moved towards the GRR where alongside and perpendicular transects cross, or they moved out of the study area as was the case for the buffalo. Elephants marginally decreased median distances to water in the late dry season in perpendicular transects (Fig. 3). These findings were basically backed up by the statistical model. The most parsimonious model (Table 2, full spec model 4) consisted of an interaction between species identity with day (juldate) and with transect classes (transect_GRR), and explained variance fairly well (R^2 marginal effects = 0.73, R^2 conditional effects = 0.77; for

estimate values see the Supporting information). The models with dietary category or observed group size per species did not improve model fit. Year of sampling also had no effect (Table 2; null model 2 with largest delta AIC). The final model was not overdispersed, although it still had heteroscedasticity in the residuals (model diagnostic plot in the Supporting information).

According to the model, species had larger distances to water in perpendicular transects than in those alongside the GRR (Fig. 3). Species distances to surface water increased as the dry season progressed especially in the drier perpendicular transects, except for buffalo which moved upstream out of the study site (Supporting information). Maximum distances of > 12 km were mainly measured for common duiker, giraffe and impala in the perpendicular transects during the late dry season.

Transect-ID included as random factor had an effect on distances to water beyond their description by fixed factors, with species on transects 4 and 6 having closer distances to water and species on transects 5 and 8 having larger distances to water than expected from the model prediction, i.e. this additional variance could not be explained by the fixed effects of the model (Supporting information). The unexpected larger distances to water in transect 8 revealed by the random effect are an artefact of this transect being less close to the GRR than other alongside transects by the GRR river bed; transect 5 was the driest part of the study area, and the closer distances to water in transects 4 and 6 are due to the fact that transect 6 was alongside the upper part of the GRR within the study area that contained flowing water throughout the year, and perpendicular transect 4 is crossed by a sand river and has two springs close by (Fig. 1).

Discussion

Although National Parks throughout Africa aim to protect wildlife from direct negative effects of human activities such as bushmeat hunting and livestock encroachment (Hofer et al. 1996, Nyahongo et al. 2005), wildlife populations within many of them are in decline because of the indirect negative effects of human activities (Ogutu and Owen-Smith 2003, Caro and Scholte 2007, Western et al. 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 within them during the dry season, which is the current situation faced by wildlife in Ruaha NP (Mtahiko et al. 2006, Stommel et al. 2016b, Roug et al. 2020). In the years of our study, due to continual evaporation, surface water by the start of the late dry season period was limited to the most upstream section of the GRR in our study site, plus small pools and water holes dug by wildlife in the dry bed of the GRR and its tributaries, and several springs. The key results of our analyses were that most species tended to stay as close to available water sources, which mainly were alongside the GRR river bed, especially at transect 6, which represents the upper section of
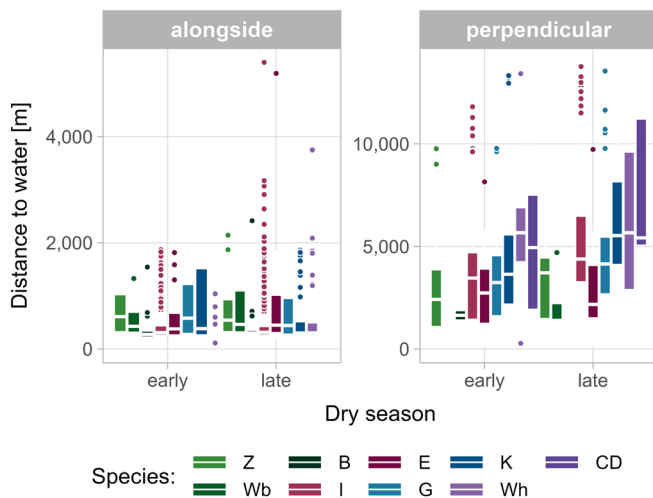

Figure 3. Median distances (meters) of nine species in transects alongside the Great Ruaha River (alongside) and transects leading away from the river (perpendicular) during the early and late dry season. The colour code indicates the dietary category: green: grazers (zebra, waterbuck, buffalo), red: mixed feeders (impala, elephant), blue: browsers (giraffe, kudu), violet: generalist species (warthog, common duiker).

Table 2. Model selection table to assess the relative contribution of the progressing drying season (juldate; consecutive number of days since 1 June), the transect location (transect_GRR; alongside or perpendicular to Great Ruaha River), species identity (species), the dietary category (diet_cat; generalist, mixed, browser or grazer) and group sizes (species_count; number of individuals in group of respective species) for the nine species on their distance to water (response variable). Transect-ID and year were included as random effect. The best models are indicated in bold as assessed by the difference of the AIC values (delta AIC), and the selected model indicated by asterisks **. df = degrees of freedom.

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	221.2
null model 2	~ 1	(1 | year)	3	5473.4
null model 3	~ 1	(1 | transect_id)	3	219.2
null model 4	~ juldate	(1 | transect_id)	4	154.6
null model 5	~ transect_GRR	(1 | transect_id)	4	904.8
full diet mod 1	~ diet_cat * juldate	(1 | transect_id)	10	99.9
full diet mod 2	~ diet_cat * (juldate + transect_GRR)	(1 | transect_id)	14	37.5
full diet mod 3	~ diet_cat + juldate + transect_GRR	(1 | transect_id)	8	73.1
full spec model 1	~ species * juldate	(1 | transect_id)	20	108
full spec model 2	~ species * (juldate + species_count) + transect_GRR	(1 | transect_id)	30	91
full spec model 3	~ juldate + (species * species_count) + transect_GRR	(1 | transect_id)	22	83.5
full spec model 4 **	**~ species * (juldate + transect_GRR)**	**(1 | transect_id)**	**29**	**4.9**
full spec model 5	**~ species * (juldate + transect_GRR) + species_count**	**(1 | transect_id)**	**30**	**0**
full spec model 6	~ species * (juldate + transect_GRR + species_count)	(1 | transect_id)	38	11.5
full spec model 7	~ species + species_count * (juldate + transect_GRR)	(1 | transect_id)	16	70
full model	~ juldate + diet_cat + species + transect_GRR	(1 | transect_id)	16	82.2

the GRR which is the only section of the GRR in our study site that contained flowing water throughout the dry season. To remain close to surface water, water dependent herbivores altered their location as surface water dried out (Supporting information). This was most noticeable in buffalo, a grazer with high water dependence that moved out of the study site apparently due to the absence of sufficient water in the GRR (Fig. 2) and least apparent in the common duiker, a generalist feeder that provided no evidence that it sought to remain near surface water (Fig. 3). Impala, kudu, and warthog also were not consistently sighted close to water sources during the late dry season, hence we conclude that these herbivores can cope with water scarcity to some degree.

Our results revealed that generalist feeders (common duiker, warthog), one mixed feeder (impala) and one browser (kudu) had significantly increased their distance to the nearest source of surface water by the late dry season (Fig. 3, Supporting information). This suggests that these species coped better with the dry season decline in surface water than grazers, mixed feeders and other browsers. The diet of common duiker generally provides sufficient water without the need to drink (Wilson 2013, Sutherland et al. 2018, Bennitt 2020) and together with physiological and behavioural adaptations to dry environments, common duiker are considered to be well adapted to dry habitats (Wilson 2013). Similarly, warthog have adaptations that provide a degree of independence from surface water. Warthogs access ground water by digging water holes (Epaphras et al. 2008, Stommel et al. 2016a) and reduce water loss by varying their daily body temperature by 7°C and sheltering in underground burrows (White 2010) when outside temperatures are high (Cumming 2013). Although previously described as water-bound (Western 1975), our results reveal that warthogs tolerated a substantial increase in their distance to surface water during the dry season. Along perpendicular transects the

mean distance of warthog to surface water was considerable with a mean of approximately 2 km (Table 2) and a maximum distance of 14 km recorded in the late dry season.

Buffalo were the most numerous grazer, zebra occurred in moderate numbers and waterbuck numbers were low (Table 1). Changes in the dry season distribution of buffalo indicate a grazer with a limited ability to cope with declining sources of surface water (Fig. 2). In the early dry season, when the entire course of the GRR in our study site contained flowing water, buffalo occurred in the alongside transects of the GRR (Fig. 2), often in large herds. By the late dry season, when the 'along' section had dried out except for small isolated pools and natural water-holes in the dry riverbed, most buffalo had left the study site (Fig. 2) for areas further upstream. Roug et al. (2020) also reported dry season movement of buffalo upstream to stretches of the GRR containing surface water and concluded the dry season loss of surface water from the GRR was a factor driving the decline in the buffalo population in Ruaha NP. Buffalo need to frequently drink and also wallow in water or mud to reduce body temperature and deter ectoparasites (Prins and Sinclair 2013). The scarcity of water pools large enough for this purpose in our study site and the large number of buffalo present in the early dry season may be linked to the large exodus of buffalo from our study site. Another large bodied grazer, the hippopotamus, is also known to leave our study site in the late dry season as the GRR dries out, probably to avoid skin damage and overheating (Stommel et al. 2016b).

Two other grazers (zebra and waterbuck) maintained larger distances to surface water than buffalo which suggests both species depend less on surface water and cope better with the dry season loss of surface water than buffalo. Contrary to expectation, zebra seemed to cope better with water absence in the late dry season; they occurred mostly alongside the GRR, but also had larger distances to water in

the perpendicular transects. Zebra dig waterholes in the dry GRR riverbed (Stommel et al. 2016a) and this behavioural adaptation may explain their presence in relatively large numbers in the dryer section along the GRR. Feeding competition with the large numbers of African buffalo (Table 1) and hippopotamus (Stommel et al. 2016a) in the upstream section may in part explain the avoidance of this area by zebra.

The number of waterbuck in our study area was low, thus interpreting the distribution of this grazer is problematic. In the early dry season, most waterbuck occurred in the upstream area of our study site (Fig. 2) but contrary to expectations, in the late dry season waterbuck shifted to include drier areas including perpendicular transects. Despite this, and in line with our prediction for grazers, plains zebra and waterbuck maintained shorter distances to water than other species that occurred along dryer perpendicular transects (Fig. 3).

Browsers should depend less on surface water than grazers but depend more on surface water than generalist feeders. Giraffe are considered relatively independent of surface water even though they do drink (Redfern et al. 2003, Ciofolo and Le Pendu 2013). Thermoregulation in giraffe is assisted by seeking shade when temperatures are high (du Toit and Yetman 2005). Greater kudu also drink but can survive without drinking provided the forage they consume contains sufficient moisture (Owen-Smith 1990, Kihwele et al. 2020). Giraffe and kudu are thought to obtain most of their moisture from browse, hence their distances to water may not be associated with their need to drink but rather their need to forage in areas with higher quality browse (James et al. 2022). In the late dry season, most giraffe and kudu were counted in the 'alongside' section of the GRR (Fig. 2). This was also true for elephant and impala (mixed feeder), zebra (grazer) and warthog (generalist feeder). This suggests that forage in this area during the late dry season may have a high nutrient and/or water content for browsers and possibly also for species in other dietary categories. 'Alongside' and 'perpendicular' areas that held most giraffe and kudu had limited sources of surface water in the late dry season, and kudu remained further away from sources of surface water than giraffe throughout the dry season. It is not known whether it was necessary for these kudu or giraffe to travel to water sources to drink.

Mixed feeders (such as impala and elephants) consume more food by browsing than grazing in the dry season than they do in the wet season. For example, the diet of elephant can change from 70% to just 25% grass and impala diet from 95% to 70% grass in the dry season (Kos et al. 2012). This increase in the intake of browse in the dry season can provide more moisture and reduce the dependence of mixed feeders on surface water, thereby making forage consumed by mixed-feeders more similar to that of browsers. In both the early and late dry season, the largest counts of impala occurred in the 'alongside' section of the GRR, with far fewer counted in the 'perpendicular' section (Fig. 2); however the few counts of impala in the perpendicular section were stable, suggesting that as sources of surface water dried out, especially in the driest area (transect 5), these impala coped with increasing distances to water. As mentioned before, vegetation in the 'alongside'

section of the GRR may contain high nutrients and/or water. Elephants occurred in all transects in the early dry season, but most were counted in the 'alongside' transects (Fig. 2). The distribution of elephants in Ruaha NP is likely to depend on access to water, as suggested for elephants elsewhere in Africa (Chamaillé-Jammes et al. 2007), because water is crucial for thermoregulation in this species (Dunkin et al. 2016). In the absence of surface water elephants can access underground water by digging holes in dry-river courses such as the GRR and its tributaries, provided the level of ground water is not too far below the surface (Epaphras et al. 2008, Stommel et al. 2016a). Unlike other large bodied species such as African buffalo and hippopotamus that can only cool their bodies when submerged in water pools, elephants cool their bodies by spraying water over themselves using water from waterholes they dig. This behavioural adaptation may in part explain why elephants were distributed throughout the study site in the late dry season, whereas most buffalo (Fig. 2) and hippopotamuses (Stommel et al. 2016b) had to move upstream out of the study site in the late dry season. It may be that the need for water to achieve thermal regulation is more important in explaining water dependence in elephants in Ruaha NP than diet.

Animal distribution

Transect counts provide an assessment of the relative importance of locations in our study site to species in different dietary categories, even though they do not provide true animal densities as our data were not statistically corrected for potential biases in detectability; thus individuals in especially small or cryptic species may have been missed in denser vegetation. Our transect data were not designed for application of formal distance sampling to account for imperfect detection (Buckland et al. 2005), because the position and number of animals were logged when first sighted to minimize potential disturbance by an approaching vehicle. Thus, measures of the perpendicular distance from animals to the transect line nor the 'true' location were recorded. However, the aim of the study was to have accurate distance measures to water.

Our data suggest that transects alongside the GRR (Table 1, Fig. 2) held generally more animals per species for most (seven of nine) species monitored than the perpendicular transects. Our findings also suggest that areas alongside the GRR contain more and/or better quality resources (water, food) and shade than those along perpendicular transects. Results of our model (Supporting information) indicate that animals in transects alongside the GRR were closer to surface water than those along perpendicular transects. This general effect depended on species and transect type, with larger differences between perpendicular transect 5 downstream, possibly because this transect connect to a section of the GRR that is the first to dry out as the dry season progress (Stommel et al. 2016a, b), and has regularly dried out each dry season in the past decades, including the exceptionally wet El Niño year of 1993 (Mtahiko et al. 2006). As a result ground water in this downstream area may occur at a greater depth than in upstream areas where perennial flow in the GRR still occurs.

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 (Owen-Smith 1996). Furthermore, water holes dug by wildlife are abandoned when they become contaminated with high bacterial loads or filled with sand, approximately 12–14 days after they were created (Stommel et al. 2016a). We think the potential errors caused by the inclusion in our model of abandoned wildlife dug waterholes that were no longer in use and the possible omission of a few such water holes used by wildlife for drinking is small.

Dry season aggregations of mammalian herbivores near sources of surface water attract large carnivores (Harrington et al. 1999, Hopcraft et al. 2005, Davidson et al. 2013) and are associated with seasonal changes in the distribution of lions *Panthera leo* and leopards *Panthera pardus* 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, close to its eastern boundary (Kalyahe et al. 2022). The accumulation of water dependent herbivores near the diminishing areas of the GRR within Ruaha NP that still hold water at the end of the dry season may increase predation rates with negative population consequence for some species. For example, in Kruger NP, artificial water sources increased the density of zebra and wildebeest, *Connochaetes taurinus* and lions in areas that were the stronghold of locally endangered roan, *Hippotragus equinus*, which increased predation of roan causing the roan population to crash (Harrington et al. 1999).

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. The case of the hippopotamus is just one example of likely consequences: the substantial loss of habitat suitable for hippopotamus as a result of the drying out of a large downstream section off the GRR (Stommel et al. 2016b) is likely to increase human–wildlife conflict in local communities outside Ruaha NP (Mtahiko et al. 2006). Large-scale upstream movements of hippopotamuses in 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 also likely to increase the transmission of a range of pathogens (Huang et al. 2022).

The GRR is considered an essential component of the ecological health of Ruaha NP (Epaphras et al. 2008, Stommel et al. 2016a, b, Roug et al. 2020). Our results also 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 forage and shade. The few small scattered pools and waterholes dug by wildlife in the downstream GRR river bed are important because no other surface water is available in this section of the GRR from approximately mid-way through the six month long dry season (Stommel et al. 2016a). The loss of surface water from an extensive area of GRR during the dry season may promote a faster decline in the nutritional quality and water content in riverside vegetation, which in turn might compromise the condition of herbivores leading to negative fitness consequences. Information on the effect of the annual loss of water from the GRR on the water table is also required.

In conclusion, the dietary niche of mammalian herbivores broadly defines their general response to human induced surface water scarcity in Ruaha NP. Generalists coped better than browsers, mixed feeders and grazers, and this was modulated by biophysical (thermoregulation in large bodies species) effects. The African buffalo is the most vulnerable species of the nine species considered to the loss of water flow in the GRR. Buffalo also are likely to suffer the largest relative habitat loss of all species considered, comparable to the habitat loss already documented in hippopotamuses (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 GRR, to avoid dry season habitat loss for numerous species. This highlights the need for a concerted action plan to create sustainable agricultural practises outside the park to reduce human–wildlife conflict over access to water and ensure the negative effects of water abstraction for crop irrigation does not come at a too high cost for wildlife (Lemly et al. 2000).

Author contributions

Claudia Schmied née Stommel: Conceptualization (equal); Data curation (lead); Investigation (lead); Validation (lead); Writing – original draft (equal). **Heribert Hofer:**

Supervision (equal); Writing – review and editing (equal). **Cédric Scherer:** Formal analysis (supporting); Visualization (lead). **Stephanie Kramer-Schadt:** Formal analysis (lead); Methodology (equal); Supervision (equal); Visualization (supporting); Writing – original draft (equal). **Marion L. East:** Conceptualization (equal); Supervision (lead); Writing – original draft (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4qrfj6qgx (Schmied née Stommel et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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