Trophic processes constrain seasonal ungulate distributions at two scales in an East African savanna

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Habitat selection is a dynamic biological process where species respond to spatiotemporal variation in resource availability. The resulting distribution patterns can be detected as presence–absence or heterogeneity in abundance and indicate habitat preferences based on environmental correlations at multiple scales. Variation in habitat selection by ungulates is constrained by trade-offs in top-down and bottom-up trophic processes arising from differences in forage requirements, water dependency, anthropogenic effects, and predation avoidance, and mediated by physiological (feeding guild) and morphological (body size) factors. We conducted distance sampling over 7 years in the Tarangire Ecosystem (TE) of northern Tanzania for six resident ungulate species: Kirk's dik-dik (*Madoqua kirkii*), Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsonii*), Masai giraffe (*Giraffa camelopardalis tippelskirchi*), impala (*Aepyceros melampus*), and common waterbuck (*Kobus ellipsiprymnus*), and tested hypotheses related to effects of top-down and bottom-up processes on ungulate presence and abundance. We modeled ecological correlates against two distributional responses to understand which environmental factors constrained these ungulate species at different scales; (i) presence–absence observations modeled in a logistic regression to assess habitat selection at an ecosystem scale; (ii) local abundances from presence-only observations modeled using a negative binomial distribution for finer-scale selection. Browser and grazer species in the TE selected suitable habitat proximal to rivers and avoided the *Combretum–Azanza* woody plant assemblage. Browsers and grazers also showed strong preference for habitat with more dense cover of preferred forage species, and abundance was influenced by the presence of specific forage species with significant seasonal variation. Mixed feeders were more heterogeneous in habitat suitability implying that broader diets allow avoidance of areas with high human activity. Small-bodied and dehydration-sensitive species selected areas near rivers and seasonal tributaries. Seasonal habitat selection was more pronounced among mixed feeders. Conservation strategies based on spatially and seasonally explicit resource selection studies such as ours can minimize impacts to biodiversity by protecting vital resources to ungulates through all seasons of the year.

Key words: habitat selection, spatial ecology, resource selection, water dependency

Ungulates play a major role in the functioning of African savanna ecosystems by regulating vegetation structure, nutrient cycling, net primary production, and fire regimes (Hobbs 1996; Augustine and McNaughton 1998; Holdo et al. 2007; Fornara and Du Toit 2008; Sankaran et al. 2013; Kimuyu et al. 2014; Palmer et al. 2015). In East African savannas, ungulate species richness is high (Olff et al. 2002), and there is substantial interspecific variation in feeding strategy, body size, and nutritional

and water requirements (Jarman 1974; Groves and Grubb 2011; Anderson et al. 2016). The distribution of ungulates reflects resource selection mediated by top-down (perceived predation risk) and bottom-up trophic processes (nutritional needs; Jarman 1974; Thaker et al. 2010; Ford et al. 2014; Anderson et al. 2016).

Our understanding of African ungulate resource selection comes predominantly from research in protected areas of South

Africa's Kruger National Park and the Serengeti Ecosystem in Tanzania, but these findings cannot necessarily be extrapolated to areas with more intensive human impacts (Cromsigt et al. 2009; Voeten et al. 2010; Burkepile et al. 2013). In many East African savannas, the past several decades have seen substantial human population growth and land-use changes from small-scale subsistence cultivation to large-scale farming, leading to habitat loss and fragmentation (Newmark 2008; Msoffe et al. 2011; Riggio and Caro 2017). Quantifying ungulate resource selection in increasingly human-influenced landscapes is crucial for evaluating the regional persistence of ungulate populations and designing effective conservation measures (Kiffner et al. 2014, 2020; Lee and Bond 2018). To facilitate these efforts, we draw upon hypotheses from studies pertaining to ungulate distribution constraints in three key areas—foraging, water dependency, and anthropogenic effects—to test predictions about resource selection in a human-influenced savanna landscape in Tanzania.

Forage constraint hypothesis.—Optimal foraging theory predicts species will select patches with greater nutritional density to maximize foraging efficiency (Brown 1988). Obligate grazers select grass-dominated areas throughout the year, and maximize nutritional content by foraging on rich soils, and habitats that facilitate grass growth (Bell 1982; Fryxell 1991; Odadi et al. 2011). As grasses mature, nutritional content and digestibility tend to decline (van Soest 1996; Esmaeili et al. 2021), resulting in resource selection influenced by body size. For example, larger-bodied ruminant grazers can more easily digest the higher biomass/poorer-quality forage than smaller-sized grazers, whose digestive systems are constrained to lower-biomass/higher-quality grasses and who therefore feed more selectively on younger plant parts (van Soest 1996; Wilmshurst et al. 2000; Esmaeili et al. 2021). In addition, variation in resource quality will influence the time needed to obtain sufficient nutrients, which can be exacerbated with higher abundances of animals due to competition (Sinclair 1985; Lima 1988; Prins 2016). Furthermore, seasonal variation in resources, for example, the loss of forage biomass on drought-deciduous plants, can cause mixed feeders (Merwe and Marshal 2012; Staver and Hempson 2020) and obligate browsers (Pellew 1983; Manser and Brotherton 1995) to utilize a greater diversity of forage species as they shift between preferred and buffer resources.

Ungulates should aggregate in areas with high-quality and abundant forage, but foraging theorists suggest ungulate herding behavior is also an adaptation to predation risk, where gregariousness improves predator detection and decreases individual time spent on vigilance (Lima and Dill 1990; Kie 1999). Both mixed feeders and browsers are also expected to encounter greater predation risk in areas with dense woody vegetation or tall grass where predator detection is inhibited, compared to grazers in more open habitats (Funston et al. 2001; Fritz and Loison 2006; Valeix et al. 2009).

If food supply primarily drives grouping dynamics, aggregation is expected to increase in locations where forage quality or quantity is higher, with more homogeneous distributions in seasons when food supply is limited and in areas of lower relative productivity (McArthur et al. 2014; Stears and Shrader 2015; Bond et al.

2019). However, if predation risk is the overriding factor in grouping dynamics, abundance should be greater in dense vegetation to improve vigilance and reduce individual risk (Thaker et al. 2010).

Water constraint hypothesis.— Interspecific differences in water dependency results in varying strengths of bottom-up constraints on ungulate distributions. The relatively low moisture content in grasses generally makes grazers more dependent on surface water than are mixed feeders and browsers (Western 1975; Cain et al. 2006; Venter et al. 2019), although physiological traits (e.g., body size, metabolic efficiency, evaporative rate) play key roles in the conditions species may tolerate (Veldhuis et al. 2019; Kihwele et al. 2020). Dependency on access to drinking water for grazers and other dehydration-sensitive species in systems with seasonal rainfall may periodically limit the distributions of such species and their access to more or different resources (Manser and Brotherton 1995; Redfern et al. 2003). Riverine habitat may also be favored by ungulate species for other services (e.g., habitat structure and forage quality), although predation risk is considered higher in such habitat (Du Toit et al. 1990; Hopcraft et al. 2005; de Boer et al. 2010).

Anthropogenic constraint hypothesis.— Ungulates might avoid human settlements as a result of the 'landscape of fear' typically associated with natural predation (Laundre et al. 2010), due to hunting by humans (Kiffner et al. 2014) and competition with human-kept livestock (Prins 2000; Odadi et al. 2011). Historically, hunting by humans has been extensive and may still continue today in some savanna ecosystems (Kiffner et al. 2014). In addition, competition with cattle for obligate grazers may also cause ungulates to avoid these areas if overgrazing or harassment from people and guard dogs acts as a deterrent (Prins 2000; Odadi et al. 2011; Bhola et al. 2012). On the other hand, areas near human settlements may form "human shields" with reduced densities of predators (Berger et al. 2001; Lichtenfield 2005; Lee et al. 2016; Bond et al. 2021). Thus, we expect avoidance to occur along a continuum that reflects the level of disturbance surrounding human settlements. Of course, if suitable habitat is only available near settlements, ungulates must seek these resources regardless of their proximity to people.

To test predictions related to the above hypotheses (Supplementary Data SD3), we used distance sampled data on ungulates collected in the Tarangire Ecosystem (TE) in northern Tanzania as a characteristic human-influenced landscape. We selected six resident ungulate species representing a spectrum of feeding strategies, water dependencies, and body mass: Kirk's dik-dik (*Madoqua kirkii*), Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsonii*), Masai giraffe (*Giraffa camelopardalis tippelskirchi* or *G. tippelskirchi*), impala (*Aepyceros melampus*), and common waterbuck (*Kobus ellipsiprymnus*; Table 1). To investigate the influence of trophic constraints and proximity to humans on ungulate distribution and abundance, we quantified resource selection in relation to season (time of year and temperature), forage availability and quality (plant species, genera, and greenness), natural predation (vegetation structure and proximity to rivers), drinking water (distance to seasonal and permanent rivers), and distance to human settlements. We

Table 1.—Physiological, metamorphic, and water dependency traits for six resident ungulate species in the Tarangire Ecosystem, Tanzania.

Species	Feeding strategy[a–c]	Adult weight (kg)[a]	Shoulder height (cm)[a]	Water dependency[b]	Global population[d]
Kirk's dik-dik (*Madoqua kirkii*)	Browser	5	35	High	Stable
Thomson's gazelle (*Eudorcas thomsonii*)	Mixed	20	70	Low	Declining
Impala (*Aepyceros melampus*)	Mixed	50	80	Mid	Stable
Grant's gazelle (*Nanger granti*)	Mixed	60	85	Mid	Declining
Common waterbuck (*Kobus ellipsiprymnus*)	Grazer	160	85	High	Declining
Giraffe (*Giraffa camelopardalis tippelskirchi*)	Browser	1,500	550	Low	Declining

[a]Gagnon and Chew (2000).
[b]Estes (1991).
[c]Cerling et al. (2003).
[d]IUCN (2021).

quantified resource selection as a function of these covariates in order to identify trade-offs between trophic processes related to nutritional requirements and predator (natural and human) avoidance. Our specific predictions about presence and abundance for each ungulate species based on the forage, water, and anthropogenic constraint hypotheses, and as related to species-specific feeding guild (grazer, browser, mixed feeder), water dependency, and body size, are as follows:

Foraging constraints.— Grazing specialists (waterbuck) will more often occupy grassy habitat year-round while mixed diet (Grant's gazelle, Thomson's gazelle, impala) and browsers (dik-dik, giraffe) will exhibit seasonally dynamic selection based on resource availability. Within the selected ranges, abundances should also positively correlate with habitats rich in desirable resources but remain seasonally dynamic reflecting nutritional variation (phenology) and threats from predation. Smaller-bodied species that feed on grasses (Thomson's gazelle, Grant's gazelle) will select for lower-biomass patches later in the growing season compared to larger grazers (waterbuck) due to requirements for more digestible plant parts.

Water constraints.— Species with high dehydration sensitivity or dependence on riparian habitat (waterbuck, dik-dik) will occupy habitat closer to the rivers and show greater abundances in these areas. Other ungulates (giraffe, impala) will remain further from rivers during the wetter months. However, seasonal reduction in water availability during the drier seasons may cause the shrinking of ranges around rivers, in which case we expected greater abundances within the occupied range further from the rivers where predator densities are lower.

Anthropogenic constraints.— Some ungulate species will select areas closer to anthropogenic dwellings and structures to avoid predation ('human shield' hypothesis) and/or to access grass during the wet season. Other species will avoid areas close to human settlements to minimise risk reflecting response to a 'landscape of fear'. Species will vary their use of areas close to human settlements seasonally to graze during the wet season when human occupation is low and avoid settlements in the dry season when the 'landscape of fear' or competitive grazing with livestock is higher.

MATERIAL AND METHODS

Study area

The climate of the TE is semiarid (Pratt et al. 1966) with three distinct precipitation periods; short rains (SR;

November–January), long rains (LR; February–April), and a long dry season (LD: May–October; Prins and Loth 1988). The commencement and quantity of precipitation vary greatly, with an annual mean of 650 mm, ranging from 312 to 1,398 mm (Foley and Faust 2010). Dominant vegetation types include heterogeneous grasslands, *Vachellia*/*Senegalia* woodlands, and deciduous *Commiphora*–*Combretum* woodlands (Lamprey 1964; Vesey-Fitzgerald 1973). We surveyed a 1,060-km² area, half of which (670 km²) occurred within the borders of the Tarangire National Park (TNP), with the remainder in Manyara Ranch Conservancy (MR) and Lolkisale Game Controlled Area (LGCA; Fig. 1). Each site differs in land management practices and human disturbances.

Data analysis

We modeled resource selection by ungulates as a function of environmental and anthropogenic covariates along 1-km transects. We created transect-specific vegetation covariates of plant type (structure) and species (food) percent cover, and calculated distance from each transect to permanent rivers, seasonal tributaries, and pastoralist temporary settlements (bomas). These covariates did not change by survey. We also quantified transect-specific vegetation greenness which varied by survey as well as survey-specific temperature for all transects. We used greenness as an index of forage biomass, with higher greenness during the long rains—the latter of two growing seasons—equating to higher biomass and lower forage digestibility (Esmaeili et al. 2021). Finally, we included season and year to account for temporal variation in rainfall and associated resource variation. We then conducted two separate analyses for each focal ungulate species using general linear mixed models (GLMMs) for (i) presence/pseudoabsence and (ii) abundance. Using GLMMs allowed us to estimate random intercepts for each transect to account for pseudoreplication.

Distance-sampling surveys

To capture seasonal variation in resource use we conducted distance-sampling surveys for ungulates at the end of each precipitation period; SR (February), LR (June), and LD (October), every year from 2012 to 2018, along 213 1-km transects distributed throughout the study area (Fig. 1). Our sampling framework encompassed three seasonal primary sampling surveys each composed of two consecutive secondary sampling surveys, for a total of six independent surveys per year (Pollock
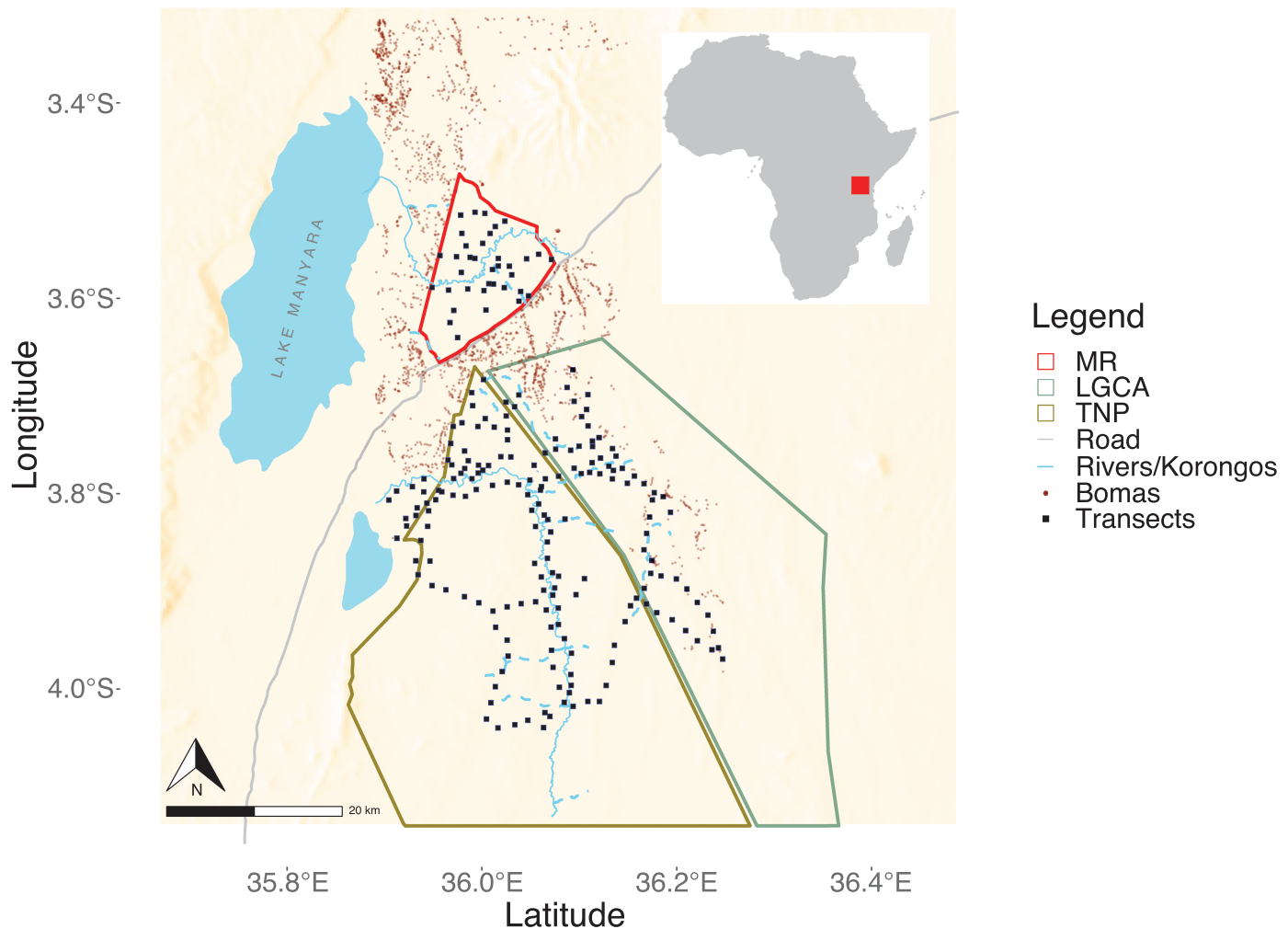
Fig. 1.—A map of the Tarangire Ecosystem, northern Tanzania. Transect locations; each represent a pair of transects made on either side of the survey trail. LGCA = Lolkisale Game Controlled Area, TNP = Tarangire National Park, MR = Manyara Ranch.

1982). No surveys were conducted after LD of 2018, for a total of 41 complete surveys. We could not assume that ungulate distributions did not change between primary and secondary surveys and thus we treated each survey as independent. For all ungulate observations we recorded a GPS point on the transect, and the perpendicular distance (m) from that point to the singleton or center of herds, measured with a laser rangefinder (Bushnell Arc 1000; Overland Park, Kansas). We recorded species and herd size for every observation. Herds were defined by observation of interindividual distance; for giraffes this was defined as <500 m, and for all other species the distance was <50 m (Kasozi and Montgomery 2020).

Accounting for imperfect detection

Observation processes may introduce excess variation in resource selection models due to imperfect detection. To correct for imperfect detection, we adjusted the raw counts for each ungulate observation using species-specific distance detection functions (Buckland 1992). Detection functions incorporated environmental covariates of vegetation greenness, relative daytime temperature, visibility, season,

and site (TNP, MR, LGCA) to improve the fit by accounting for heterogeneity within a survey (Marques and Buckland 2004; Marques et al. 2017). Model selection was based on lowest Akaike's Information Criterion (Akaike 1979) value. We tested for goodness-of-fit with the Cramer–von-Mises test and visual assessment in a quantile-quantile plot (Burnham et al. 2004). We truncated data to remove observations at distances that yielded <0.15 detectability that are subject to the highest levels of inaccuracy (Marques and Buckland 2004). We adjusted each herd size observation by dividing the observed count by the detection probability for that observation based on the detection function. We could not account for imperfect detection in presence/absence data since individuals could have moved between the intraseasonal samples (i.e., each transects' population was not closed between samples).

Vegetation surveys

In 2014, we conducted a ground-based vegetation survey at the center of each of the 213 transects. At every location we quantified

the percent cover of each woody species and grass based on visual estimation in two plots, one on each side of the road. Plots were 50 × 20 m, starting 10 m from the road. We also estimated visibility at each transect by averaging the distance in meters that a laser rangefinder penetrated the vegetation from five repetitions on each side of the road at 1 m above ground. We summarized the data at each transect by using the mean values from the two plots.

Environmental covariates

Vegetation.— Using our ground-based vegetation measurements, we identified three woody plant assemblages using network analysis of co-occurrence and assigned percent cover of each woody plant assemblage at each transect. To determine association among plant species (Supplementary Data SD1), we created a "checkerboard" association matrix, computing the *c*-score for each species combination using the *bipartite* package (Stone and Roberts 1990; Dormann et al. 2008) in R (Version 4.0.2, R Core Team 2020). We built this matrix from a subset of the woody plant species seen >5 times (*n* = 27) to maximize accuracy of edge weights. Using the matrix, we graphed the network, and conducted community detection analysis with the *igraph* package for R (Csardi and Nepusz 2006). We used the cluster-walktrap algorithm to allocate woody plant assemblages, and calculated *Q* as a measure of the strength of modularity between assemblages (Clauset et al. 2004).

Greenness.— To account for variation in detectability from seasonal greenness and for use as a covariate to resource selection, we extracted the transect-specific Normalized Difference Vegetation Index (NDVI) from the preprocessed eMODIS V6 product (Jenkerson et al. 2010) at a several day temporal resolution; dates were chosen so as to have maximum overlap with each survey period. The spatial resolution of the NDVI data was 250 m. We calculated distance from the center of each transect to the nearest permanent and seasonal rivers using GIS software (QGIS Development Team 2020) to determine proximity to water sources and dry season green vegetation. We used Google Earth (Mountain View, California) aerial imagery from June 2014 to map human settlements (bomas) as points as an index of anthropogenic effects.

Temperature.— Ungulate activity is known to vary depending on ambient temperatures (Jarman and Jarman 1973; Leuthold and Leuthold 1978; Klein and Fairall 1986; Owen-Smith 1998). To account for effects of temperature on detection we extracted land surface temperature (LST) from the Moderate Resolution Imaging Spectrometer (MODIS) database for each survey day. The LST data set had a daily temporal resolution and 6-km spatial resolution (Wan et al. 2015). From the LST we also calculated the relative day temperature as:

$$T_r = T_t - \frac{T_{t-1} + T_{t-2} + T_{t-3}}{3}$$

where the relative temperature (T_r) is calculated by subtracting the mean of the previous 3 days' temperature from the temperature on the day of observation (T_t). Negative and positive values of T_r indicate whether the day was anomalously cold or warm, respectively, relative to the three preceding days.

Resource selection

We modeled both occurrence and abundance using the *glmmTMB* package for R (Brooks et al. 2017). Presence/pseudoabsences were modeled as a binomial response variable composed of a "1" for any single or herd of ungulates observed, and a "0" if not, using logistic regression. Repeat sampling from the same transects over multiple surveys was dealt with by including a random intercept term for transect in all GLMMs. We scaled all covariates (Supplementary Data SD2) by subtracting the mean and dividing by the standard deviation to facilitate model convergence. Due to the large number of plant species that constitute some species' diets as identified in previous studies, we ran preliminary models to identify which plant species and genera explained the greatest variance using the Bayesian information criterion (BIC; Schwarz 1978) step-down selection. Using the plant species and genera identified in this preliminary step, we then built a final model including other variables we considered ecologically important in describing resource selection of the focal ungulate species. We performed BIC step-down selection again on the final model until the most parsimonious structure was found. We included year and season in models for any species when they improved the model fit, and tested interactions with season when the relationship was deemed appropriate for a specific species.

To model abundance response, we used only presence observations (total count per transect > 0) with a negative binomial distribution due to overdispersion estimated using the *DHARMa* package for R (Hartig 2020). To ensure the response variable contained zeroes, we subtracted one from each abundance observation as required for negative binomial distributions.

We cross-validated models using a *k*-fold test with 10 folds and reported the root mean square error. We tested multicollinearity among covariates in final models using the *performance* package for R (Lüdecke 2018) and did not include two variables with high collinearity in the same model.

Results

In the TE we observed 18 resident species within our distance-sampling transects, with six having sufficient frequency of detections for analyses: Kirk's dik-dik (*n* = 324 herd detections), Grant's gazelle (*n* = 154), Thomson's gazelle (*n* = 83), giraffe (*n* = 542), impala (*n* = 1,007), and common waterbuck (*n* = 211). We counted giraffes only until 2015. More observations were made during the dry season (*n* = 862), than in the short (*n* = 789) or long wet seasons (*n* = 670). We identified 76 different plants in the transects: 32 to the level of species. All resource selection models showed suitable levels of fit and robustness for all six targeted ungulate species unless identified. Generally, our logistic regression models for presence explained greater variance owing to larger sample sizes (Fig. 2).

Environmental covariates

Vegetation.— The cluster-walktrap algorithm parsed the plant network into three modules (Supplementary Data SD1), representing woody plant assemblages in our study area (Supplementary Data SD1). Modularity *Q* was 0.30, indicating a moderately good division of the network. Woody plant assemblages
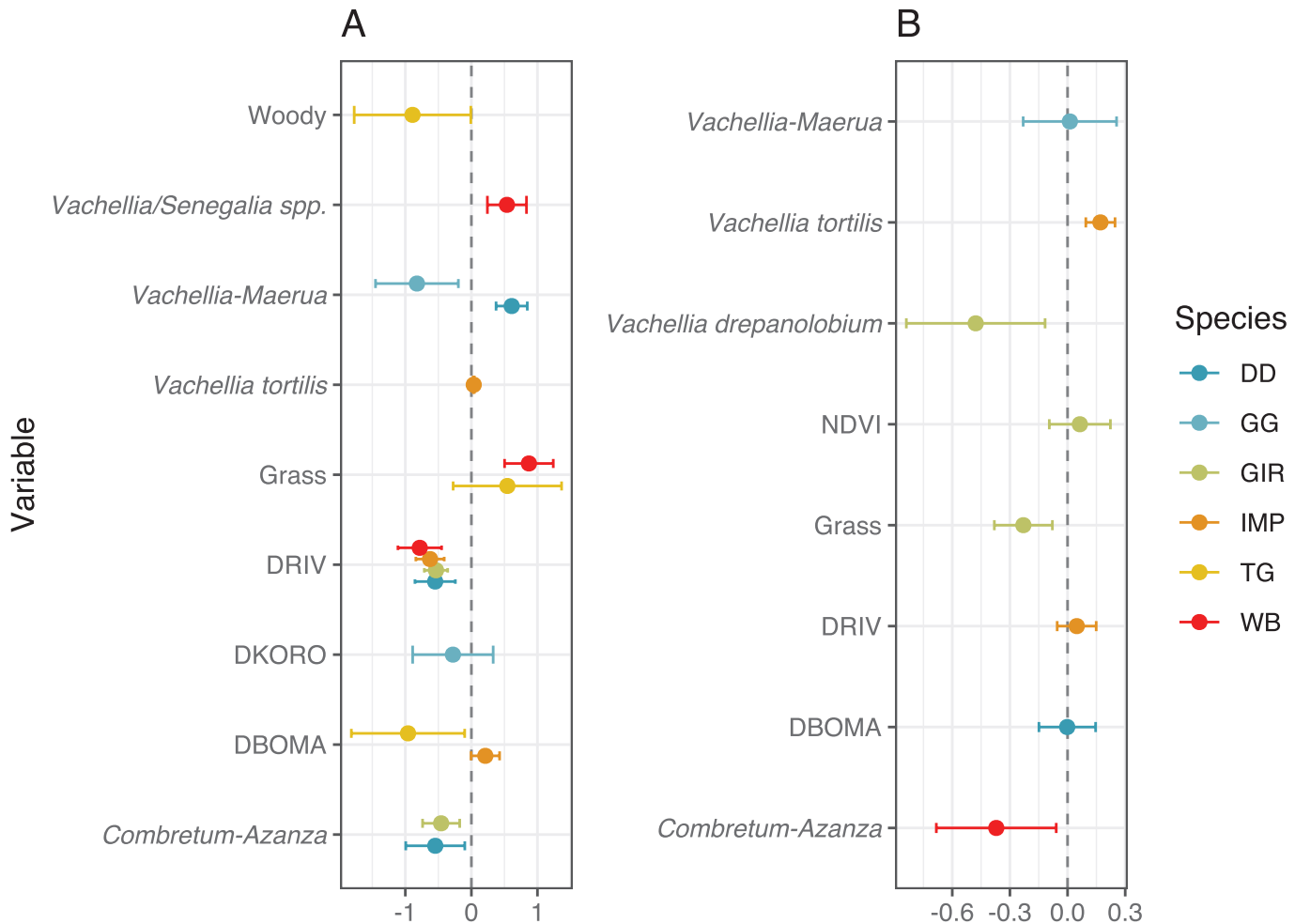
Fig. 2.—Coefficient plot for each species showing all environmental covariate effects from the presence (A) and abundance (B) models, excluding interactions with season and year. DD = dik-dik (*Madoqua kirkii*), GG = Grant's gazelle (*Nanger granti*), GIR = Giraffe (*Giraffa camelopardalis tippelskirchi*), IMP = Impala (*Aepyceros melampus*), TG = Thomson's gazelle (*Eudorcas thomsonii*), WB = Waterbuck (*Kobus ellipsiprymnus*). Woody = woody vegetation, DRIV = distance to nearest river, DKORO = distance to nearest seasonal tributary, DBOMA = distance to nearest temporary human settlement (boma), NDVI = Normalized Difference Vegetation Index, a measure of greenness. Data collected in the Tarangire Ecosystem, Tanzania from 2012 to 2018.

were: *Dichrostachys–Balanites* (DB) of which the greatest average proportions were represented by *Dichrostachys cinerea* (0.30), *Commiphora* spp. (0.17), and *Balanites aegyptiaca* (0.12). The DB woody plant assemblage had the smallest average grass cover (53.5 ± 32.6%), and a distribution predominantly in the northern part of the study region (Supplementary Data SD1). The *Vachellia–Maerua* (VM) woody assemblage was characterized by high proportions of *Vachellia tortilis* (0.53) and had intermediate grass cover (61.4 ± 35.4%). The VM woody assemblage occupied the largest part of the study region especially near the rivers. The *Combretum–Azanza* (CA) woody assemblage had a high proportion of *Combretum* spp. (0.47), had the highest average grass cover (67 ± 30.3%), and was found in isolated areas in the southwest and central-east.

Detection functions

All detection functions had the greatest amount of variation explained by interactions between season and visibility covariates, except for dik-dik which was best explained with just

season (Supplementary Data SD4). Stratifying by site improved model fit for dik-dik, giraffe, and impala (Supplementary Data SD4) but not for Grant's gazelle, Thomson's gazelle, and waterbuck (Supplementary Data SD4). All models for every species were deemed valid from the Cramer–von-Mises test (*P* > 0.05) indicating the detection function was not significantly different from the observed distance observation distribution.

Constraint outcomes

We found support for our foraging constraint hypothesis for giraffe, impala, and waterbuck (Supplementary Data SD5 and SD6). Giraffe abundances were higher in *Vachellia drepanolobium*-dense transects during the long rainy season (Fig. 3) and less abundant in areas with more grass cover (Supplementary Data SD6), with considerable seasonal and yearly variation (Fig. 3). Giraffes also occupied areas with lower CA assemblage cover. Impalas were more abundant in areas rich in *V. tortilis*, with support from candidate models that this varies seasonally

(Supplementary Data SD6). Waterbuck presence was positively tied to greater cover of grass and *Vachellia* and *Senegalia* species (Supplementary Data SD5). Transects with the highest CA assemblage coverage had the lowest waterbuck abundances (Supplementary Data SD6). We found no support for our foraging constraint hypothesis in dik-dik, Grant's gazelle, and Thomson's gazelle distributions. However, we found significant positive and negative effects on dik-dik presence in the VM and CA vegetative assemblages, respectively (Supplementary Data SD5). Grant's gazelle presence also showed a negative response to the VM assemblage (Supplementary Data SD5). Neither presence nor abundance for any species was significantly correlated with NDVI.
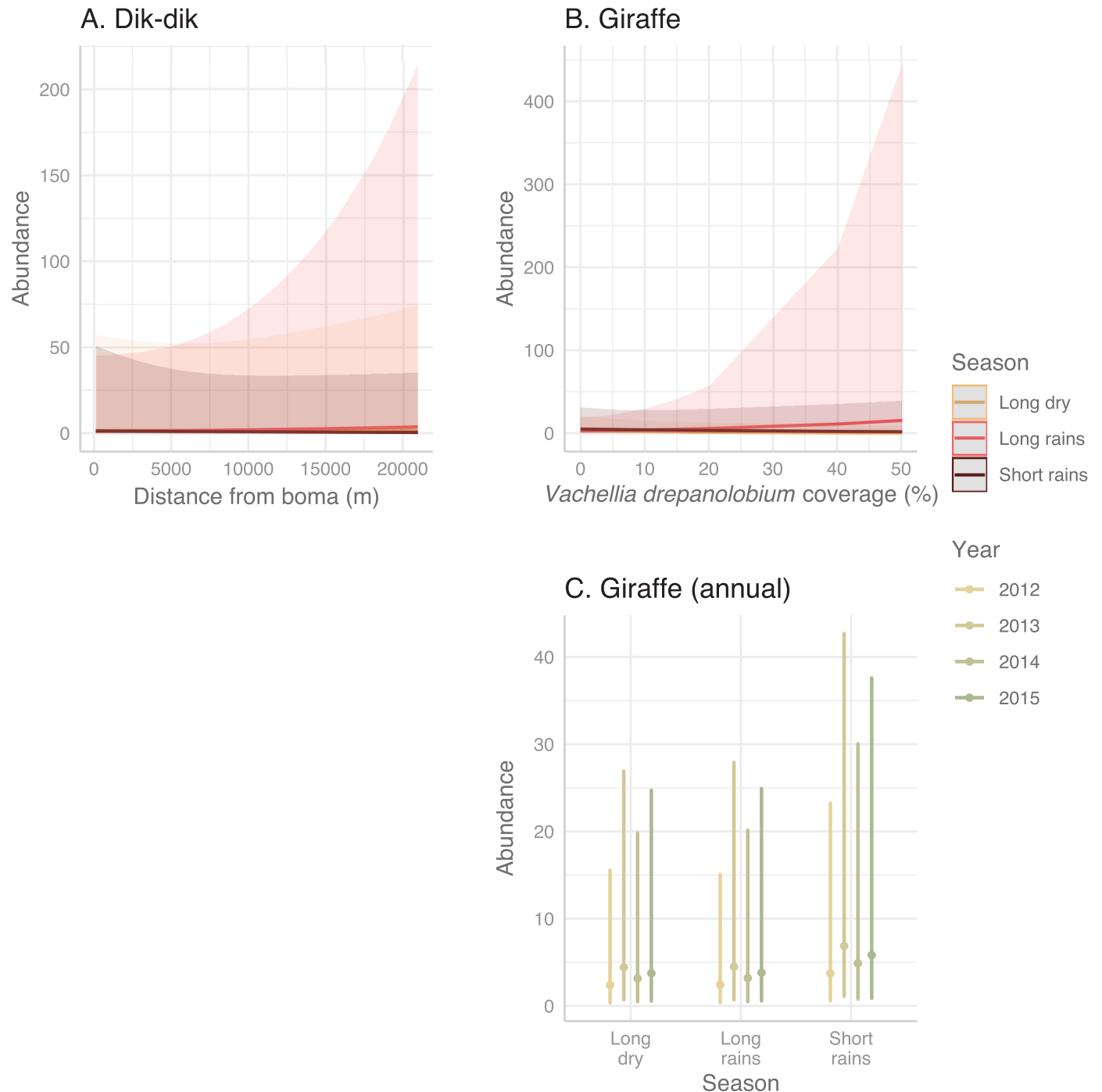

Fig. 3.—Abundance model predictions. Dik-dik (*Madoqua kirkii*)—Seasonal responses in abundance to distances from bomas in the dik-dik populations (A). Giraffe (*Giraffa camelopardalis tippelskirchi*)—Changes in abundance as predicted from an interactive effect between *Vachellia drepanolobium* cover percentage and season in the giraffe population (B). Giraffe (annual)—Changes in abundance as per year and season in giraffe population (C). Data collected in the Tarangire Ecosystem, Tanzania from 2012 to 2018.

Dik-dik, impala, and waterbuck distributions supported the water constraint hypothesis with less evidence for Grant's gazelle. Dik-diks selected areas closer to rivers, with a significant decrease in distance from rivers during the dry season (Fig. 4). Giraffe, impala, and waterbuck presence was significantly higher at locations closer to the rivers (Supplementary Data SD5). Grant's gazelles showed variance in their affinity for seasonal tributaries, increasing only during the short rainy season (Fig. 4). No support was found for giraffes and Thomson's gazelle for the water constraint hypothesis.

We found support for our anthropogenic constraints in dik-dik and Thomson's gazelle and some evidence in impala. Dik-diks avoided areas near bomas in the short rains season (Fig. 3) and we recorded significant variation in both seasonal and yearly presence (Fig. 4). Impalas tended to occupy areas further from bomas during the dry season and short rains, but closer to bomas during the long rainy season (Fig. 3). Thomson's gazelles showed significantly higher presence closer to bomas and significantly less in areas with higher densities of woody species (Supplementary Data SD5). No evidence was found for giraffe, Grant's gazelle, or waterbuck for our anthropogenic constraint hypothesis.

DISCUSSION

Our study provides unique insight into two outstanding features of ungulate resource selection in human-influenced landscapes. First, we identify human presence as an influential factor on both distribution and abundance of several resident ungulate species, including dik-dik, Thomson's gazelle, and to some extent impala. This distribution behavior may be shaped by the 'landscape of fear' in response to variation in perceived predation risk, either natural or anthropogenic. Second, dependency upon drinking water appears to span across the ungulate species regardless of feeding strategy and body mass.

Overall, our study shows that trophic processes constrain ungulate distributions at the ecosystem scale and abundances within the range of species. Regarding foraging constraints, we found support for our prediction that obligate grazers such as waterbuck will remain in grassy habitat year-round. However, our prediction of seasonal switching of forage resources in mixed feeders and browser strategists was only supported with giraffe and impala. We found no support for smaller-bodied grazers avoiding areas with high vegetation greenness at the end of two growing seasons. For water constraints, we found dehydration-sensitive species (waterbuck, dik-dik) remained near rivers as we hypothesized. We also found support for our hypothesis of greater proximity to the rivers in dik-dik as well as impala during the long dry season. Unexpectedly, we found giraffes were proximal to rivers year-round which may be a result of greater forage quality in these areas and lower perceived predation threat for these mega-herbivores. Our anthropogenic constraint hypotheses were supported in dik-dik as well as in impala, which avoided areas near human settlements (bomas) during the dry season yet used these areas during the wet season. Similarly, our predictions were supported by the finding that Thomson's gazelles remain proximal to bomas year-round, although we discuss alternative explanations for this behavior below.

Dik-dik distributions in the TE appear to be bottom-up driven by both forage and water constraints. As dik-diks maintain territories year-round and require access to drinking water, their distribution must inherently include access to permanent water sources (Maloiy and Barrington 1973). The highest aggregations were near rivers in the dry season in support of our water constraint hypothesis. We suspect dik-diks avoid high interspecific browsing competition that occurs near rivers during the dry season by selective foraging that facilitates niche partitioning (Kartzinel et al. 2015). We also demonstrated evidence of range expansion further from rivers during the wetter seasons which is aided by the availability of temporary waterholes and surface water. This behavior affords dik-diks opportunity to seek forage more widely in the wetter seasons. Manser and Brotherton (1995) found similar compensatory behavior in dik-diks that forwent nutritional and energy budgets to consume forage with high water content in the dry season (e.g., *Combretum*), then shifted to more nutritional forage as water became more accessible.

We found that giraffe distributions were driven by bottom-up processes related to foraging constraints that fluctuated seasonally, in support of our predictions (Fig. 4; Supplementary Data SD5). However, their presence in areas near rivers was not supported. We explain these giraffe distributions by considering feeding strategy and the nonuniform distribution of resource quantity and quality. For example, Bell's (1971) catenary gradient describes how key browse genera such as *Vachellia* and *Senegalia* have higher palatability and nutrition in high browser-traffic areas such as near natural water ways (Du Toit et al. 1990). We also detected no significant increase in presence of giraffe near rivers during the dry seasons, signaling their lack of dependency on water sources (Kihwele et al. 2020). However, intraspecific competition for food may limit local abundances during the dry months (Bond et al. 2019). This was supported by our finding that giraffes form smaller aggregations in the dry season where *V. drepanolobium* concentrations are high, which is a major browse species for most giraffe populations (Foster and Dagg 1972; Du Toit 2003). Thus, we suggest that nutritional content of forage constrains the distribution of the TE giraffe population, while predation threats to adults are probably negligible given their large body size. These results provide insight into the mechanism of giraffe fission–fusion dynamics in the TE, where bottom-up effects from yearly and seasonal rainfall fluctuations result in significant changes in abundance to manage intraspecific foraging competition based on nutrient density (Fig. 4).

We found no conclusive evidence for any constraint hypotheses in our Grant's gazelle models. We did find the *Vachellia–Maerua* woody plant assemblage to be significantly avoided. However, Grant's gazelles have a strong northern bias in their distribution in the TE, which correlates with volcanic soils of potentially greater nutritional quality of forage (Bell 1982).
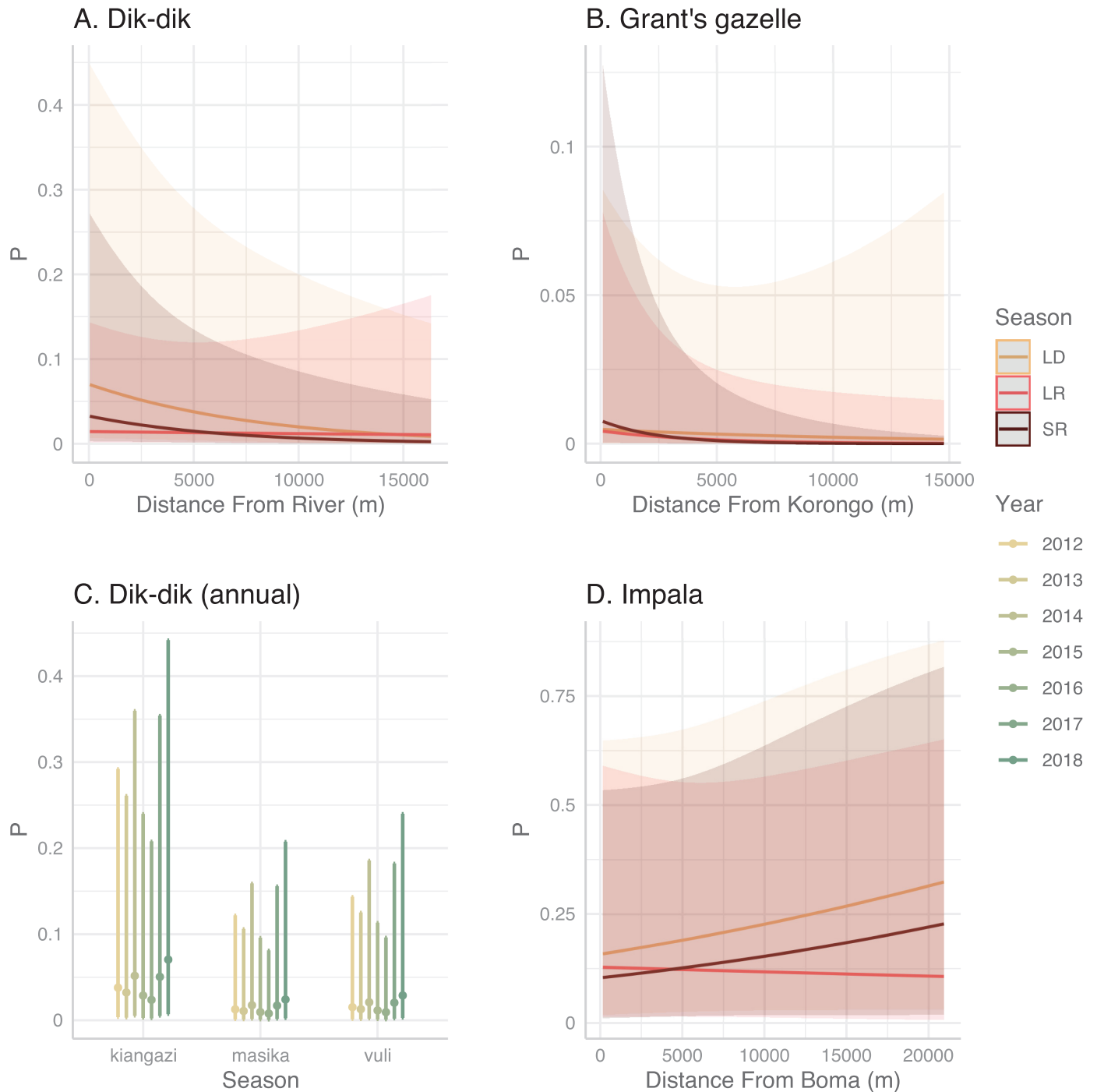
Fig. 4.—Presence model predictions. Dik-dik (*Madoqua kirkii*)—Seasonal responses to distance from rivers in the dik-dik population with 95% confidence intervals (A). Grant's gazelle—Interactive effect on presence between distance from tributaries and season in the Grant's gazelle (*Nanger granti*) population (B). Dik-dik (annual)—Changes in presence per season and year in the dik-dik population (C). Impala (*Aepyceros melampus*)—Interactive effect on presence between distance from rivers and season for the impala population. *P* = probability of presence (D). Data collected in Tarangire Ecosystem, Tanzania from 2012 to 2018.

Since Grant's gazelles maintain this distribution year-round, they may also switch from favored forbs and grass forage in the wet season to browse in the dry season, which has been observed elsewhere (Stewart and Stewart 1971; Spinage et al. 1980; Hansen et al. 1985). However, with our current data set this was not detectable due to a low number of observations and

lack of spatially explicit information on herbaceous vegetation species.

Our larger data set for impalas provided a more detailed understanding of bottom-up and top-down constraints, which appears to vary with resource availability. Our finding of high presence and abundance in areas rich in *V. tortilis* was echoed

in several dietary studies (Jarman 1976; Dunham 1980; Du Toit et al. 1990; Miller 1996) and provides strong support for the foraging constraint hypothesis. Thus, we suggest that this tree plays an important role as a browse and seed pod buffer resource when grass is less available in the TE. Impalas also are much more likely to occur near-natural water sources, as found in this and other studies (Young 1972; Smit et al. 2007). Interestingly, we detected larger abundances further from the rivers year-round which contradicts our hypothesis of only seasonal constraints due to water sources. Based on physiological and trait assessments, impalas are not particularly susceptible to dehydration (Maloiy and Hopcraft 1971; Kihwele et al. 2020). Thus, we believe this distribution describes trophic trade-offs between accessing quality forage near permanent water sources and avoidance of the associated predation risks (Du Toit et al. 1990; Redfern et al. 2003; de Boer et al. 2010). Impalas had a lower presence near bomas during the dry season in support of our anthropogenic hypothesis of poaching avoidance. However, there are two alternate explanations. Firstly, as observed in other impala studies, this result might be due to low forage availability or quality near bomas (Augustine 2010; Merwe and Marshal 2012). Impalas have a capacity and tendency to switch from grazing to browsing as the dry season progresses which would also explain this behavior (Fritz et al. 1996; Merwe and Marshal 2012; Kos et al. 2012). Secondly, the dry season also coincides with peak cattle grazing which may signal low resource availability through interspecific competition with livestock. Indeed, the sustainable management of cattle grazing in African savannas is a contentious topic, with potential for positive and negative outcomes (Augustine 2010; Fynn et al. 2019) and great dependency upon yearly variations in resource availability influenced by precipitation (Odadi et al. 2011; Bhola et al. 2012).

For Thomson's gazelle we found evidence supporting our anthropogenic constraint hypothesis that the species will occupy areas near bomas due to the 'human shield' effect (Supplementary Data SD5) similar to female giraffes with calves (Bond et al. 2019). Little interspecific competition between livestock and Thomson's gazelle further supports this hypothesis (Kiffner et al. 2020). It is possible that Thomson's gazelles only occur in nutrient-rich areas of ecosystems which, in the TE, are mostly occupied by humans. Thomson's gazelles are technically mixed feeders but predominantly feed on grasses, switching to browse during dry seasons (Estes 1991; Cerling et al. 2003). Previous studies in other regions demonstrated that Thomson's gazelle distributions were restricted by both predator avoidance and access to high-quality grasses (Stelfox and Hudson 1986; Fryxell et al. 2004; Anderson et al. 2016; Fryxell and Berdahl 2018). For example, avoidance of dense woody vegetation simultaneously decreases predation risk (Thaker et al. 2010) and increases the potential for grass cover which Thomson's gazelles tend to prefer (Estes 1991). We did not measure grass height in this study, but future research in the TE would benefit from examining relationships of presence and abundance of Thomson's gazelle and other smaller ungulates with grass height, given its demonstrated impact on predator evasive behaviors (Costelloe and Rubenstein 2018). Although we expected Thomson's gazelle distributions to be constrained by access to

water, we found no support of this. We suspect they drink mostly at waterholes (Smit et al. 2007) and may spend little time near rivers due to the drastically increased threat of predation (Owen-Smith 1992; de Boer et al. 2010; Ogutu et al. 2010).

Waterbucks in the TE showed the strongest water constraints to their distribution. Waterbuck is considered one of the species most sensitive to water availability (Melton 1983; Redfern et al. 2003). In previous studies, waterbucks preferred rivers over artificial waterholes (Smit et al. 2007; Smit 2011) suggesting that riparian areas provided other resources in addition to drinking water. Smit (2011) predicted that finer-scale selection within this riverine distribution may be discernible with higher resolution data. As waterbucks are obligate grazers (Hofmann and Stewart 1972; Gagnon and Chew 2000) we tested this prediction and demonstrated higher abundances in grass-rich habitat. This result also supported our predictions of forage constraints on grazers. Waterbuck presence was also higher in areas with greater concentrations of *Vachellia* and *Senegalia* spp. which we attribute to the greater numbers of these genera near rivers. We also found seasonal fluctuations in presence, with a slight reduction during the wet season, similar to Kiffner et al. (2016, 2020). Our study provides insights into the habitat and resource requirements of the TE resident ungulate populations and how these requirements constrain the distribution of each species. We show that distance to water sources is a useful proxy. Other studies have produced this proxy using combined functional traits (Veldhuis et al. 2019; Kihwele et al. 2020). We identify bottom-up processes stemming from the year-round flowing rivers and associated habitat as one of the most important features in the TE. Furthermore, yearly and seasonal fluctuations in presence and abundance indicate that resident ungulates in the TE are sensitive to both short- and long-term variation in precipitation and thus are potentially vulnerable to low rainfall years. This effect may be exacerbated in areas where livestock are grazed. A recent study also indicated that compositional changes and declines in diversity of ungulate populations may result from changes in water availability (Veldhuis et al. 2019). As such we highlight that a key focus of research and management should be river water sources and associated riverine habitat, and the ways in which these resources will be increasingly shared as the human population grows. Given the acutely vulnerable state of waterways in human-influenced landscapes resulting from contamination, run-off, damming, and irrigation (Ramsar Convention on Wetlands 2018), protection of this resource may be among the most important conservation measures for ungulate persistence.

This research also revealed that vegetative assemblages, genera, and species have unique relationships with the distribution of each ungulate species, with little overlap among a diverse suite of ungulates. Seasonal variation in access to different resources was also evident. Thus, maintaining vegetative diversity to provide structural and nutritional heterogeneity both spatially and temporally for multiple species is also of great importance—particularly in providing year-round resources through the fluctuations in phenological cycles of different vegetative clades as well as the freedom of movement for wildlife to access the different resources as they change in relative value seasonally and annually.

Understanding resource selection patterns of ungulates—especially in regions increasingly dominated by anthropogenic impacts—will facilitate more effective conservation and sustainable management of these ecologically and economically critical taxa. As such, conservation strategies based on spatially explicit resource selection studies are critical to minimize impacts to biodiversity and maximize local economic benefits derived from these systems (Shackleton et al. 2007; Sachedina 2008; Rija 2009).

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Vegetation assemblage network analysis plot, vegetation assemblage distributions, plant associations, and proportional cover of each species/genus per assemblage type.

Supplementary Data SD2.—All variables used in both distance detection function and resource selection function models.

Supplementary Data SD3.—Further explanation of constraint hypotheses and species predictions.

Supplementary Data SD4.—Detection function and candidate model parameters.

Supplementary Data SD5.—Final presence model parameters per species.

Supplementary Data SD6.—Final naïve abundance model parameters per species.

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