Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

# Patterns and predictors of ungulate space use across an isolated Miombo woodland reserve

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**Keywords**
black rhinoceros; camera trapping; fire frequency; habitat fragmentation; habitat use; Malawi; occupancy modelling; water dependence; large herbivores.

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Editor: Femke Broekhuis
Associate Editor: Martin Leclerc

Received 24 March 2022; revised 25 January 2023; accepted 9 February 2023

doi:10.1111/jzo.13059

## Abstract

Understanding ecological- and management-related predictors of mammal space use within protected areas is critical for management planning. This is particularly true in small, fenced and isolated reserves where we hypothesised that management-related activities will influence large herbivore space use more than ecological characteristics. We used camera trap data to assess the space use patterns for 18 ungulate species in the small and isolated Majete Wildlife Reserve (Majete) in the understudied Miombo woodland ecoregion of southern Malawi. In the 2018 dry season, the 691 km$^2$ reserve was systematically surveyed for ungulate presence at 140 camera trap locations. Over a period of 5456 camera days, the survey yielded 11 078 independent detections of 18 ungulate species and three predators. Using a single-species occupancy modelling framework, the probability of space use of ungulates was assessed in relation to five management (fire exposure, fire frequency, water availability, distance from fence and road) and five ecological (visibility, grass biomass, vegetation type, terrain ruggedness and predator abundance) space use covariates, while accounting for imperfect detection. Top-ranked models contained multiple covariates for 15 of the 16 species modelled, with only nyala's (*Tragelaphus angasii*) space use best predicted by vegetation type only. Distance to water, vegetation type, visibility and fire frequency were predictors having strong influences on six or more species each. More management-related covariates reflected in top models, but ecological covariates had more meaningful effect sizes making us reject the hypothesis. Importantly though, distance from the roads and fence were also identified as prominent predictors. Notably, black rhinoceros' (*Diceros bicornis*) probability of space use increased with distance from the reserve boundary. Beyond informing habitat management for ungulates in Majete, these results can form the basis for understanding species-specific space use patterns in other small reserves with similar characteristics and threats.

## Introduction

Historically, the African landscape was home to large populations of mammals (Harris et al., 2009; Hempson et al., 2017). However, increasing human population numbers and the associated effects of urban and agricultural expansion have altered this picture with most large mammal populations, and specifically ungulates, now largely confined to protected areas (Caro & Scholte, 2007). Reserves have consequently become critical for the conservation of extant ungulate populations (Wegmann et al., 2014), but even here they may be at risk (Caro & Scholte, 2007). Since the 1970s there has been a 50% decline in ungulate population abundance within African reserves (Western et al., 2009), attributable mainly to over-hunting and habitat conversion (Caro & Scholte, 2007; Craigie et al., 2010), as well as poor management such as inadequate infrastructure maintenance and law enforcement (Lindsey et al., 2014). To successfully conserve existing ungulate populations within the confined space of reserves, management-related and ecological processes that drive ungulate species space use needs to be better understood (Rich et al., 2016).

Habitat fragmentation due to increasing human settlement, roads and fences has led to a loss of connectivity between habitats, with reserves being isolated and static natural remnants of habitats (Newmark, 2008), susceptible to anthropogenic edge effects which strongly influence patterns of biodiversity

persistence (Lindsey et al., 2014; Ramesh et al., 2016; Tobler et al., 2015). For example, mammal species presence often increases further away from anthropogenic activity close to reserve boundaries (Rich et al., 2016, 2017; Wang et al., 2015), but there are exceptions where some species thrive due to reduced predation or anthropogenic food availability (Fischer et al., 2012). Fear of anthropogenic activity reduces the effective reserve size with potential knock on effects for population viability and conservation (Rich et al., 2016). Fencing reserves is often considered a solution to protect biodiversity from negative human impacts such as poaching (Hayward & Kerley, 2009). However, fences create an artificially closed and confined space, which limits space, food and water resource availability (Newmark, 2008), creating the need for more intensive management of these populations and their environment by applying actions such as prescribed burns and providing water artificially (Hayward & Kerley, 2009; Miller et al., 2015; Selier et al., 2018).

Savanna ecosystems are difficult to manage as isolated, fenced systems due to their intrinsic heterogeneous and dynamic characteristics (Gaylard et al., 2003). Typically, small fenced reserves (<1000 $km^2$; Miller et al., 2015) require intensive management to maintain viable habitat for ungulates (Hayward et al., 2007; Massey et al., 2014). Water provision and fire management become important management interventions, but also influence ungulate space use (Bond & Archibald, 2003; Owen-Smith, 1996). The spatial and temporal manipulation of surface water availability influences ungulate movements and drives the localised impact of grazing on vegetation and soil around water sources (Smit et al., 2007). Fire frequency can lead to variation in the structure and composition of different vegetation types, with frequent fires reducing woody vegetation and increasing the grassy layer, while the absence of fire may result in increased tree canopy (Bond et al., 2005). The manipulation of fire to mimic natural fire regimes and prevent the spread of wildfires therefore influences ungulate distribution, which in turn influences predation risk (Anderson et al., 2007; Doherty et al., 2022). Reserve infrastructure such as roads similarly influence ungulate landscape use with some ungulate species avoiding roads due to the risk of humans and vehicles (Fahrig & Rytwinski, 2009; Leblond et al., 2013; Muposhi et al., 2016).

Ungulate conservation success is affected by the ecological characteristics of the reserve (Illius & O'Connor, 2000). Rainfall and soil nutrients regulate the quantity and quality of food availability, which is used differently by ungulates with varying metabolic requirements (du Toit, 1995; Jarman, 1974). Vegetation types differ in species composition, structure, climatic conditions and soil nutrients (de Cáceres & Wiser, 2012) which influence ungulate landscape use. Predator presence alters prey behaviour, which may result in the creation of a landscape of fear (Laundré et al., 2010). Specifically, ungulates tend to avoid areas of real or perceived risk and/or alter habitat use in relation to predator presence (Tambling et al., 2015; Thaker et al., 2011). Many management-related and ecological factors influence the space use of ungulates, with species potentially showing unique relationships, dependent on each species specific characteristics such as diet and body size (Jarman, 1974). Furthermore, considering the decline of ungulates in reserves despite conservation efforts (Craigie et al., 2010), an understanding of these space use predictors is important, especially as large mammal reintroductions, including ungulates, is increasingly considered an essential component of reserve restoration (Cromsigt et al., 2018).

Majete Wildlife Reserve (Majete) is a small fenced reserve (691 $km^2$) situated in the Miombo Woodland Ecoregion of south-west Malawi. The reserve is surrounded by rural settlements, and poaching was rife during the second half of the 20th century with the majority of large mammals eradicated. However, since the organisation African Parks took over management in 2003, conditions improved with effective anti-poaching measures and the reintroduction of locally extinct ungulate species (including black rhinoceros and elephant *Loxodonta africana*; Briers-Louw et al., 2019; Staub et al., 2013). Majete is one of the last few intact reserves in Malawi, and is recognised as a successful restoration project (Briers-Louw et al., 2019; de Vos et al., 2020). However, how the restored ungulate populations use Majete in reaction to management and ecological drivers, is not clear. This information is essential to further improve conservation efforts in this small, isolated reserve where some ungulate populations need to be manipulated due to space constraints. Furthermore, there is a paucity of published research on the ecology and distribution patterns of medium and large ungulates in Miombo woodland habitat, but see Caro (1999).

In this study we assessed the space use patterns of ungulates in Majete and the predictors thereof, by using a systematic camera trap survey and an occupancy modelling framework. We hypothesise that in this small reserve where management interventions are common, the effect of management-related activities will be more influential on large herbivore space use than ecological characteristics.

## Materials and methods

### Study area

Majete has three distinct seasons based on temperature and rainfall: the hot wet season (November to April), cool dry season (May to August) and the hot dry season (September to October). Average annual rainfall is 680–800 mm in the lower lying eastern areas (approximately 150 m.a.s.l) with the higher lying western slopes (approximately 455 m.a.s.l) receiving 700–1000 mm (Wienand, 2013). The mean minimum and maximum temperatures are 12.5 and 26.3°C in June and 20.9 and 34.8°C in November (Martin, 2005). Soils have low nutrient potential which together with the rainfall gradient, influence the species composition and vegetation structure (Frost, 1996). Six vegetation types are recognised —high altitude tall miombo woodland in the west of the reserve gradually changes into a more open mixed tall woodland in the centre and east, with riverine and thicket vegetation associated with streams and rivers in the extreme east of the reserve (Frost, 1996; Sherry, 1989; Fig. 1). There are nine known natural springs and 10 artificial waterholes, with two perennial rivers transecting the north-east corner of the reserve (Fig. 1).

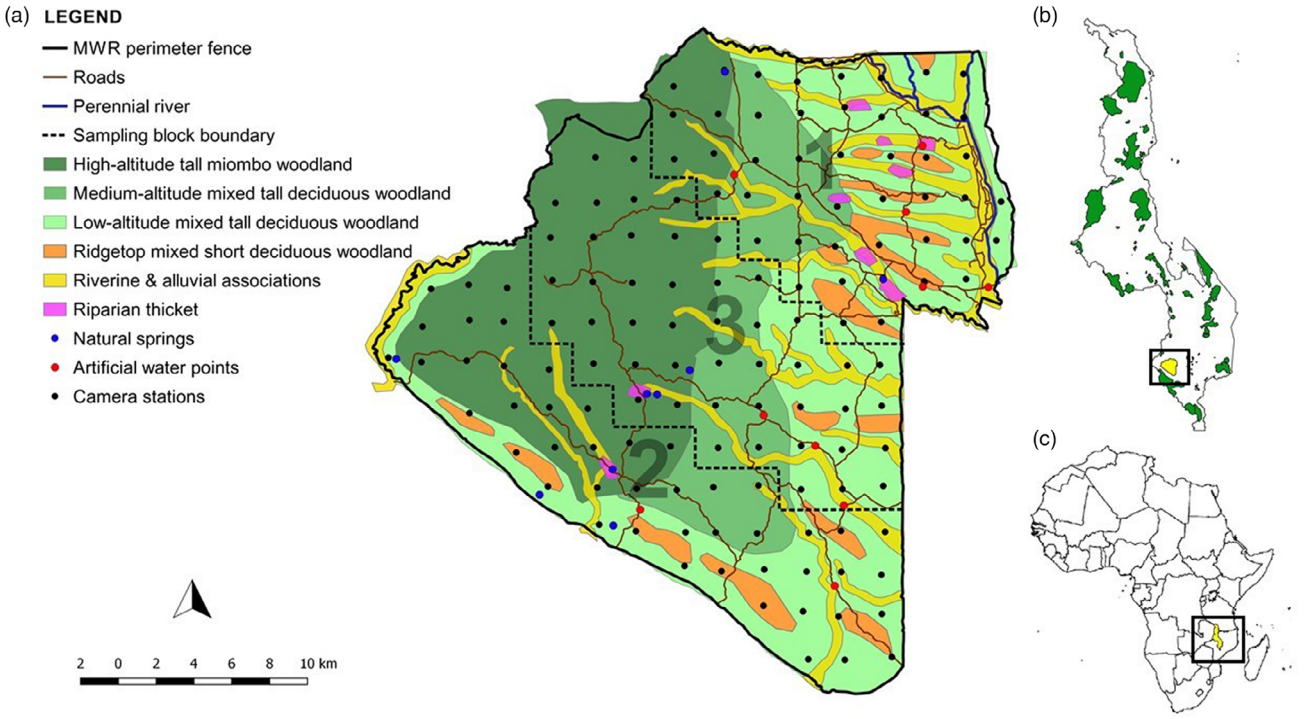


**Figure 1** (a) Map of Majete Wildlife Reserve (Majete) indicating the perimeter fence line, roads, vegetation types, distribution of surface water and the 140 locations where cameras were placed to determine the space use of ungulate species. The reserve was surveyed in three phases by dividing the area into three blocks (dotted line) which were each surveyed for 40 days before moving on to the next block. The sequence of sampling is indicated by the displayed number and took place between June and December 2018. (b) The location of Majete (boxed yellow area) in relation to other protected areas (green areas) within Malawi, (c) location of Malawi within Africa (boxed).

The road network (Fig. 1) supporting low levels of tourism, is concentrated in the north eastern section, with roads in the remainder of the reserve used for management and research purposes.

## Survey design

The camera trap survey took place during the dry season of 2018. A systematic camera trap array of 140 camera trap locations (Fig. 1), identified as the centre points of 5 $km^2$ grid blocks, and thus set 2 km apart, were surveyed in three consecutive phases of 47, 47 and 46 locations each. At each location one camera (Cuddeback X-Change™ - Model 1279 with a white LED flash) was deployed, unbaited, inside a protective metal case. Three photographs were taken at each camera event during the day and one at night allowing the flash to recharge; the detection zone was set to wide view. Cameras were secured to trees, approximately 50 cm above the ground, within 10 m of the most used wildlife trail in close proximity to the predetermined camera trap location points (Colyn et al., 2018). To confine the survey to the dry season, and hence limit seasonal variability in space use in reaction to rainfall, we restricted the sampling period for each block to 40 days. The first block was surveyed between June and August, the second between July and September and the third between September and December. For more detail on the survey design see Reece et al. (2021).

## Predictors of space use

Both management-related and ecological covariates that could influence ungulate space use were investigated. This was done by jointly modelling the detection probability and presence/absence of species to evaluate the effect of site covariates on occupancy by using single-species occupancy models (Mackenzie et al., 2006). We investigated the 'probability of use' ($\Psi$) rather than 'probability of occupancy' as the assumptions of closure and independence (Mackenzie & Royle, 2005) were not met due to some species' home ranges considered to be larger than a single 5 $km^2$ survey site. As occupancy models correct for imperfect detection, detection probability ($P$) was modelled as a function of site-specific covariates thought to impact species detectability (Sollmann, 2018). Four detection variables were considered at each camera location, namely vegetation density, distance to fence, terrain ruggedness and trail usage (Table 1). Eleven ecological- and management-related covariates were hypothesised to influence the probability of ungulate space use and measured at each camera location. The variables were visibility, grass biomass, vegetation type, immediate fire response, fire frequency, distance to water, distance

**Table 1** The variables used to predict ungulate detection probability and space use, with the unit of measure, range of values, and data type indicated, as well as the motivation for use of the variable, the methods used to measure the variable, and references associated with it. See Appendix S1 for more detail.

| Variable | Unit/range/data type | Variable motivation | Methodology | References |
|---|---|---|---|---|
| Distance to fence | Metres<br>410–9995 m<br>Continuous | **Detection**: human-related objects (i.e. cameras) may be avoided more readily close to fence due to negative anthropogenic exposure on fenceline<br>**Space use**: Mammals may be deterred from areas close to fenceline due to anthropogenic disturbance | Used the NNJoin Plugin and conducted Nearest Neighbour Analysis in QGIS | Rich et al. (2016), QGIS Development Team (2018) |
| Vegetation density (detection)<br>Visibility (space use) | Metres<br>9.25–81 m<br>Continuous | **Detection**: Vegetation density could influence species use of trails<br>**Space use**: Ambush predator hunting success may improve with increasing grass height and vegetation cover | Distance where the lower part of an assistant became obscured by vegetation. Average of four measurements in four directions from camera | Hay et al. (2008) |
| Terrain ruggedness | Terrain ruggedness index<br>0.25–16.63<br>Continuous | **Detection**: Degree of terrain concavity or convexity can affect animal movement and consequent detection<br>**Space use**: Terrain accessibility can govern space use | Using the Terrain Ruggedness Index (TRI) and Digital Elevation Model, each camera location was assigned a TRI value | Anderson et al. (2010), Puri (2015), Riley et al. (1999), Sappington et al. (2007) |
| Trail usage | Level 1, 2 or 3<br>Categorical | **Detection**: Level of trail use may influence the likelihood of a species being detected | Trail associated with camera assigned a score: 1—trail with no animal signs. 2—Trail with minimal signs. 3—Trail with abundant signs. | Mann et al. (2015), Colyn et al. (2018) |
| Grass Biomass | tons/ha<br>0–27 tons/ha<br>Continuous | **Space use**: A measure of grass forage availability | The comparative yield/dry weight rank method. Average of a biomass score (1 to 9) assigned to four quadrats (1 × 1 m) located 10 m from camera in four directions | Shipley (1999), Haydock and Shaw (1975), Friedel et al. (1988) |
| Vegetation type | Six vegetation types (Fig. 1)<br>Categorical | **Space use**: Vegetation types vary in vegetation structure, as well as quantity and quality of forage | Cameras assigned to one of the six vegetation types | du Toit (1995), de Cáceres and Wiser (2012), Sherry (1989) |
| Immediate fire response | Burnt/unburnt<br>Categorical | **Space use**: Recently burnt areas may attract ungulates due to changes in forage quantity, quality and vegetation density. May also change vulnerability to predation | Camera site categorised as burnt or unburnt. If burnt during camera deployment the area was recorded as burnt | Hopcraft et al. (2005), Anderson et al. (2007), Doherty et al. (2022) |
| Fire frequency | No. of times burnt between 2001 and 2019<br>0–10<br>Categorical | **Space use**: Fire frequency change woody structure and plant species composition affecting habitat and dietary preferences and anti-predator strategies | The number of times a 30 ha grid cell burnt between 2001 and 2019 used as proxy for fire frequency at camera site | Bond et al. (2005), Anderson et al. (2007), Smit and Prins (2015), Nieman et al. (2021) |
| Distance to water | Metres<br>81 – 9941 m<br>Continuous | **Space use**: Species water dependence influences space use in relation to surface water availability | Used the NNJoin Plugin and conducted Nearest Neighbour Analysis in QGIS | Redfern et al. (2003), QGIS Development Team (2018) |
| Distance to road | Metres<br>2–3706 m<br>Continuous | **Space use**: Mammals may favour roads for movement or avoid them | Used the NNJoin Plugin and conducted Nearest Neighbour Analysis in QGIS | Fahrig and Rytwinski (2009), QGIS Development Team (2018) |

**Table 1** Continued

| Variable | Unit/range/data type | Variable motivation | Methodology | References |
|---|---|---|---|---|
| Slope | Degrees<br>0–34°<br>Continuous | **Space use**: Mammals may avoid or prefer steep slopes | The Slope feature in QGIS Terrain Analysis Tools in QGIS and the DEM | Oberosler et al. (2017), Ahumada et al. (2013), QGIS Development Team (2018) |
| Relative large predator abundance | Relative abundance index<br>0–22.5<br>Continuous | **Space use**: The presence of the large predators, viz: lion, leopard and spotted hyaena may influence the space use of some herbivore species | The independent detections of the three large carnivores were combined and divided by sampling effort and multiplied by 100. Leopard was excluded for buffalo, zebra and eland as these species do not form part of leopard diet in Majete | Rich et al. (2017), Radloff and du Toit (2004), le Roux et al. (2018), Briers-Louw and Leslie (2020) |

to fence, distance to road, terrain ruggedness, slope and relative large predator abundance (Table 1).

## Modelling framework

Photographs were collated by one person using the camera trapping software Camelot 1.4.5 (Hendry & Mann, 2018). The 35 detected species (see Reece et al., 2021 for full species record) were then filtered to include only large predators (lion *Panthera leo*, leopard *Panthera pardus* and spotted hyaena *Crocuta crocuta*) and the 18 ungulate species captured.

Binary matrix detection histories were created using the independent captures (filtered using 30-min intervals to ensure independence; Davies et al., 2016) of respective species at each camera station. To estimate species detection probability, the detection history was condensed from the 40 sampling days into eight sampling occasions, where any presence in a 5-day period was counted as one in the detection history (Bischof et al., 2014). Collinearity between the covariates was assessed using variance inflation factors (VIFs) in the R package car, version 3.0–9 (Fox & Weisberg, 2019). If a covariate had a VIF value of >5 it was considered to covary with another (Dormann et al., 2013) and the most pertinent covariate was retained. Following the VIF assessment, slope and terrain ruggedness covaried, and thus we omitted slope. The retained continuous covariates were scaled into standardised *z*-scores for all analyses (Comley et al., 2020).

Single-species occupancy models (Mackenzie et al., 2006) were used to estimate species-specific detection probabilities and probability of use using the R package unmarked, version 0.13–1 (Fiske & Chandler, 2011). We estimated detection probability in the absence of detection covariates and species with detection probabilities of <0.15 were not considered for further analysis as they produce probability of use estimates considered inaccurate (O'Connell et al., 2006; Rogan et al., 2019). At this stage klipspringer (*Oreotragus oreotragus*) and Sharpe's grysbok (*Raphicerus sharpei*) were removed from further analysis as they did not meet the 0.15 detection criteria. Important detection covariates for each species were determined by first measuring detection with each covariate and retaining the covariate with the lowest AIC value (Akaike, 1974; Burnham & Anderson, 2002). We then sequentially added additional variables until no covariate that was added produced an AIC value improvement of >2. The detection covariate, or additive combination thereof, which resulted in the most parsimonious top detection model was retained for estimating probability of use and the predictors thereof.

In the probability of use modelling process, space use covariates were allowed to vary, with all possible linear additive combinations of covariates assessed, while holding the detection covariates estimated in the previous section constant, that is, $\Psi$ (covariate), $P$ (covariate). Where mathematical convergence issues were encountered due to too few detections for a categorical variable, the variable was removed from further analysis. This occurred once resulting in the removal of the fire and vegetation variables from the modelling of hippopotamus (*Hippopotamus amphibious*). Once all possible models were run we identified plausible top models from the complete model set as those that were within ΔAIC of two of thse best performing model as determined from the AIC value. Further investigation of the predictors of space use were then limited to these plausible models and we present all plausible models in our results.

To visually display the importance of a single predictor variable on a species space use, the remaining variables in the top model were held constant at their median so that probability of use was allowed to vary (from minimum to maximum observed value) as a consequence of just that single variable in question. We estimated predicted probability of presence for each of the plausible top models and averaged these model predictions (Cade, 2015) to obtain an aggregated response for each variable identified in the top model sets. The resulting probability of use (including 95% confidence intervals) of the single variable was then plotted against the range of values for the specific covariate, making it possible to assess how the probability of use changed as a function of the covariate. Across all model scenarios we then tallied the number of occasion management and ecological characteristics respectively influenced the different ungulate species space use as a measure of the relative contribution management and ecological covariates make to ungulate space use. Further to this we used the magnitude of predicted change in space use to differentiate between potentially informative and uninformative parameters (Arnold, 2010). If a covariate present in the plausible top models of a species influenced such a species space use by at least 10% over the full range of possible values for that parameter, it was considered as informative and if not, it was considered an uninformative parameter. To understand which of management or ecological variables had the larger meaningful affect, we summed the number of times a variable was considered as informative across all species. All statistical analyses were performed in R software, version 3.6.1. (R Development Core Team, 2019).

## Results

A total of 5456 camera days yielded 120 239 photographs, of which 11 078 were independent detections of 18 ungulate species (10 938 detections; Table 2) and 140 detections of the three large predator species (14 lion, 43 leopard and 83 spotted hyaena).

### Detection probability

Warthog had the highest detection probability ($P$ = 0.79, SE = 0.01), followed by impala ($P$ = 0.56, SE = 0.02), kudu ($P$ = 0.51, SE = 0.02) and waterbuck ($P$ = 0.47, SE = 0.02; Table 2). The detection of reedbuck, eland and buffalo were unaffected by the measured detection covariates while all the other species were influenced by one or more of the covariates (Table S1).

### Probability of use

The probability of reserve use ($\Psi$) for the 16 ungulates retained for analysis ranged from 0.15 to 0.95 (Table 2). Kudu was most widely distributed, using approximately 95% of Majete ($\Psi$ = 0.95, SE = 0.02), followed closely by warthog ($\Psi$ = 0.94, SE = 0.02). Hippopotamus ($\Psi$ = 0.15, SE = 0.05) and reedbuck ($\Psi$ = 0.22, SE = 0.04) had the narrowest distribution within Majete.

**Table 2** The number of independent detections, probability of detection ($P$) and probability of use ($\psi$) estimates for the ungulates that were detected during the camera trap survey at Majete Wildlife Reserve. The detection estimates of klipspringer and Sharpe's grysbok are included but no further analyses were performed for these species

| Species | No. of detections | $P \pm$ SE | $\psi \pm$ SE |
|---|---|---|---|
| African elephant *Loxodonta africana* | 267 | 0.26 ± 0.02 | 0.61 ± 0.05 |
| Black rhinoceros *Diceros bicornis* | 47 | 0.18 ± 0.03 | 0.23 ± 0.05 |
| Bushbuck *Tragelaphus scriptus* | 562 | 0.40 ± 0.02 | 0.63 ± 0.04 |
| Cape buffalo *Syncerus caffer* | 626 | 0.44 ± 0.02 | 0.54 ± 0.04 |
| Common duiker *Sylvicapra grimmia* | 460 | 0.37 ± 0.02 | 0.72 ± 0.04 |
| Common eland *Tragelaphus oryx livingstonii* | 192 | 0.23 ± 0.02 | 0.47 ± 0.05 |
| Common reedbuck *Redunca arundinum* | 55 | 0.19 ± 0.03 | 0.22 ± 0.04 |
| Greater kudu *Tragelaphus strepsiceros* | 1043 | 0.51 ± 0.02 | 0.95 ± 0.02 |
| Hippopotamus *Hippopotamus amphibius* | 31 | 0.33 ± 0.06 | 0.15 ± 0.05 |
| Impala *Aepyceros melampus* | 1100 | 0.56 ± 0.02 | 0.5 ± 0.05 |
| Klipspringer *Oreotragus oreotragus* | 17 | 0.14 ± 0.05 | |
| Lichtenstein's hartebeest *Alcelaphus lichtensteinii* | 160 | 0.26 ± 0.03 | 0.4 ± 0.06 |
| Nyala *Tragelaphus angasii* | 165 | 0.36 ± 0.03 | 0.32 ± 0.05 |
| Plains zebra *Equus quagga* | 598 | 0.44 ± 0.02 | 0.60 ± 0.052 |
| *Sable Hippotragus niger* | 773 | 0.44 ± 0.02 | 0.83 ± 0.03 |
| Sharpe's grysbok *Raphicerus sharpei* | 64 | 0.12 ± 0.02 | |
| *Warthog Phacohoerus africana* | 3510 | 0.79 ± 0.01 | 0.95 ± 0.02 |
| Waterbuck *Kobus ellpsiprymnus* | 1268 | 0.47 ± 0.02 | 0.64 ± 0.05 |

### Predictors of space use

Plausible model sets (i.e. models within ΔAIC < 2 of the top model) ranged from a single model (nyala) to 15 models (impala – Table S1) with an average of seven models. The collection of plausible models per species included up to nine covariates (buffalo and waterbuck) and as few as one for nyala. However, if we consider the covariates that are informative (that result in >10% change in probability of use) we find the number of influential covariates per species drops markedly (Fig. 2). Impala space use is then predicted to be influenced by the highest number of covariates (six) followed by eland and zebra with five covariates each. Most (94%) of the informative parameters are also present in more than 50% of the

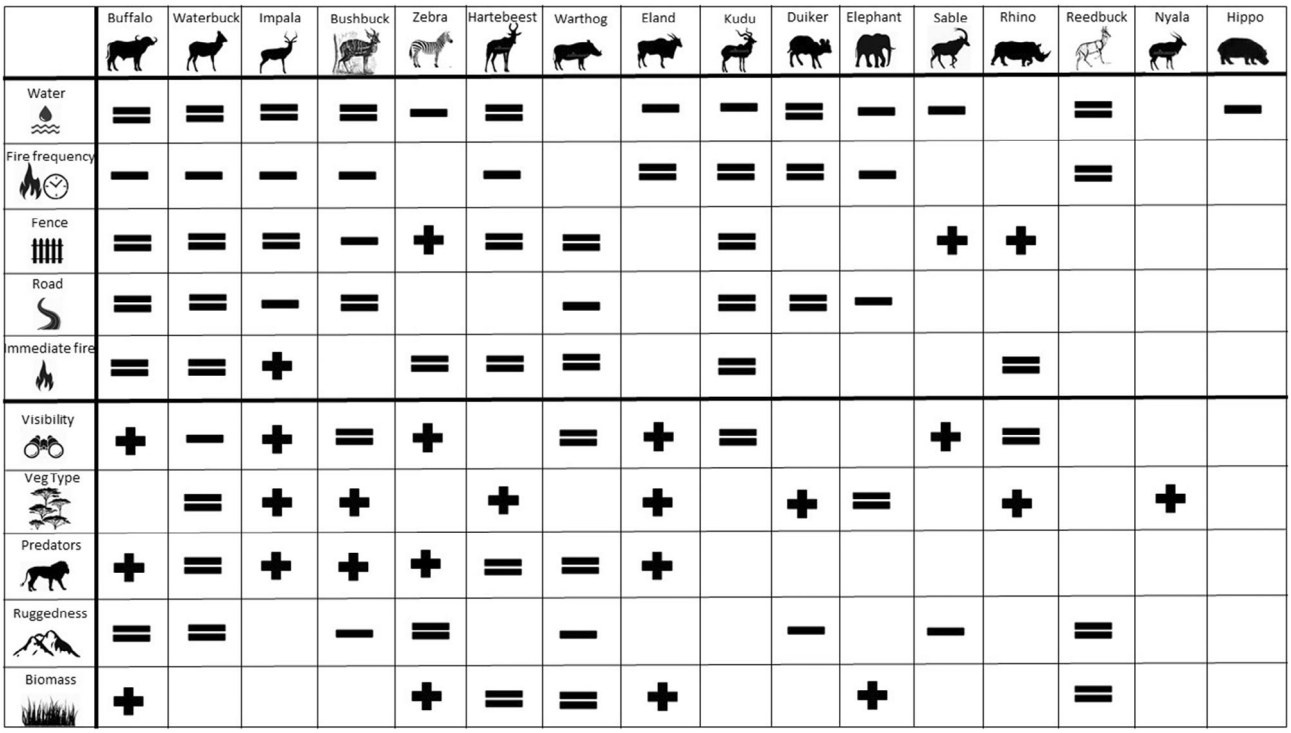


**Figure 2** Management and ecological covariates effect on ungulate species space use. A '=' sign indicates that a covariate was present in at least one of the best models explaining a particular species space use (Figs. S1-S14). A '+' or '−' sign indicates not only the presence of such a variable in the best model output for the species but also that it is considered an informative parameter (change of more than 10% in space use across the measured variables range), with the direction of the relationship indicated by the '+' or '−'. For the two categorical variables a '+' sign indicates a difference of more than 10% in space use between recently burnt or unburnt areas or a 10% difference in use of at least two vegetation types. The species are ordered from those influenced by the most number of variables to the least. Management-related covariates are at the top of the figure and ecological covariates below them, ordered from most influential to least.

plausible models. Out of a possible 80 correlations between the five management-related variables and 16 ungulate species, 49 were retained in plausible models, while the model output for the five ecological covariates indicated 42 of a possible 80 correlations (Fig. 2). However, if we consider the number of informative interactions, the ecological characteristics have more meaningful correlations than the management-related covariates (26 vs. 20, Fig. 2).

When considering management-related predictors, distance to water influenced the highest number of species (13; Fig. 2) and is considered informative for zebra, eland, kudu, elephant, sable and hippo (Fig. 3a-f) with a reduction in space use further from water. Fire frequency influenced 10 species and is informative for buffalo, waterbuck, hartebeest, bushbuck, elephant and impala (Fig. 3g-l) which all use areas that were less frequently burned, more. Distance to fence also influenced 10 species, and was an informative parameter for sable, zebra, bushbuck and black rhinoceros (Fig. 3m-p). Distance to road influenced eight species and was informative for warthog, elephant and impala, with a negative influence (Figs. 3q-s). The immediate effect of fire influenced eight species but was only informative for impala which used unburnt areas more (Fig. 3p).

Considering the ecological covariates, visibility influenced 10 species, but was informative for buffalo, sable, waterbuck, zebra, eland and impala where all but waterbuck were influenced positively (Fig. 4a-f). Vegetation type influenced nine species, with hartebeest, bushbuck, duiker, black rhinoceros, eland, impala and nyala strongly influenced by vegetation (Fig. 4g-m). Predator presence influenced eight species, and was an informative parameter for buffalo, zebra, bushbuck, eland and impala which all positively associated with predators (Figs. 4n-r). Terrain ruggedness influenced eight species, but was considered informative for only sable, bushbuck, duiker and warthog which all use less rugged terrain more (Fig. 4s-v). Grass biomass influenced seven species, and was considered informative for buffalo, zebra, eland and elephant, which all associate strongly with increasing grass biomass (Figs. 4w-z).

## Discussion

In Majete, ungulate space use is influenced by both management-related and ecological variables with no single predictor impacting all species. Although management-related covariates reflected in more top models than ecological covariates,

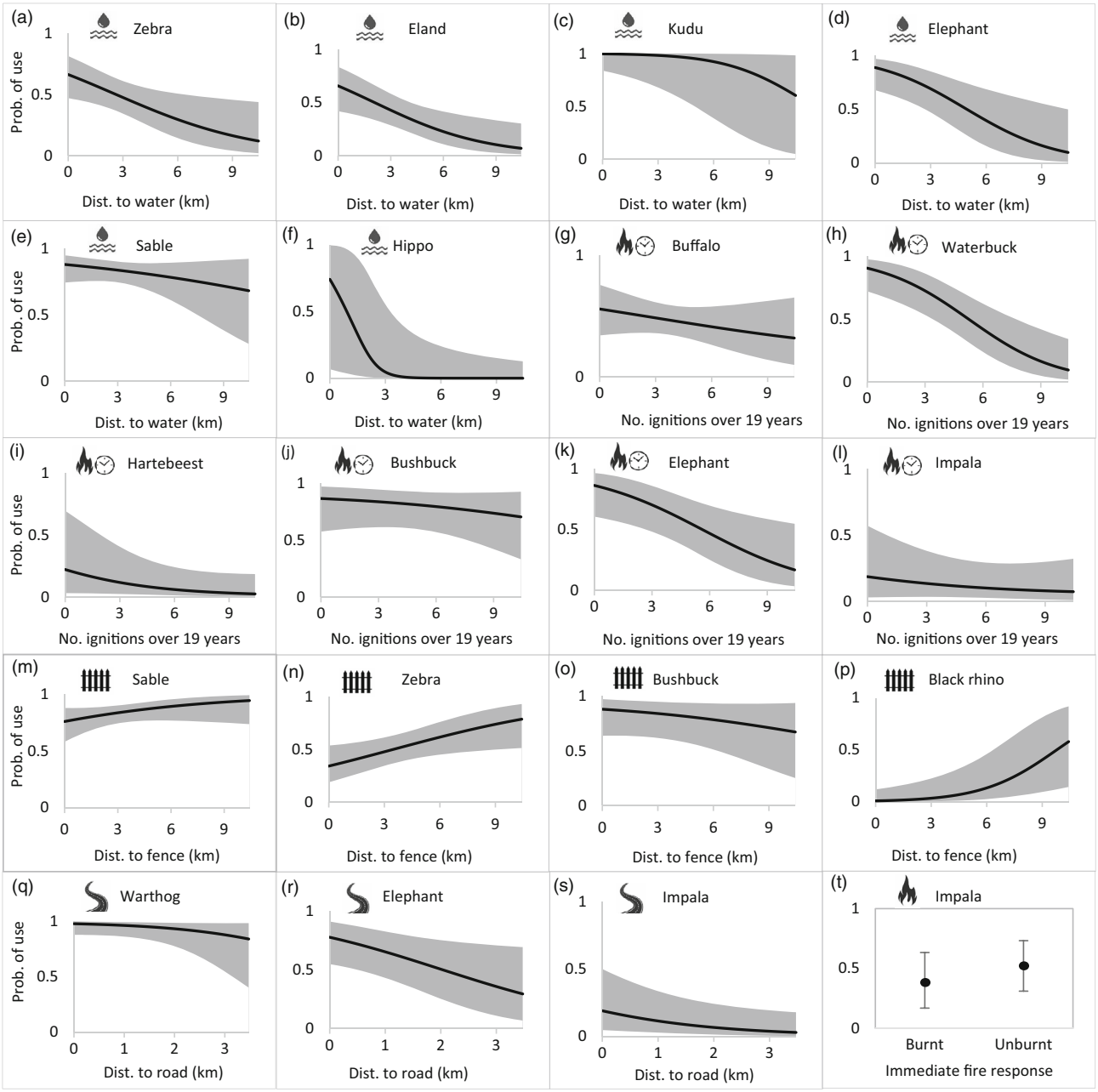


**Figure 3** Species-specific plots (a-t) of management-related covariates effect on ungulate space use (95% confidence intervals in grey). Only covariates from the plausible top models per species that influenced such a species space use by at least 10% over the full range of possible values for that parameter (See Table 1 for detail on each variable) are presented here, as they were considered to be truly informative (see text for more detail). The covariates are represented by the following symbols on each species-specific plot: = Distance to water, = Distance to road, = Distance to fence, = Immediate fire response, = Fire frequency.

more ecological covariates were considered to be informative and hence we rejected the hypothesis that management-related attributes are more influential in the small and isolated Majete. However, our study does confirm that anthropogenic activities within and around a reserve influence ungulate space use, an observation noted not only in Africa (Fuda et al., 2018; Mkonyi et al., 2018), but also at a global scale (Cavada et al., 2019; Rich et al., 2016; Schuette et al., 2013).

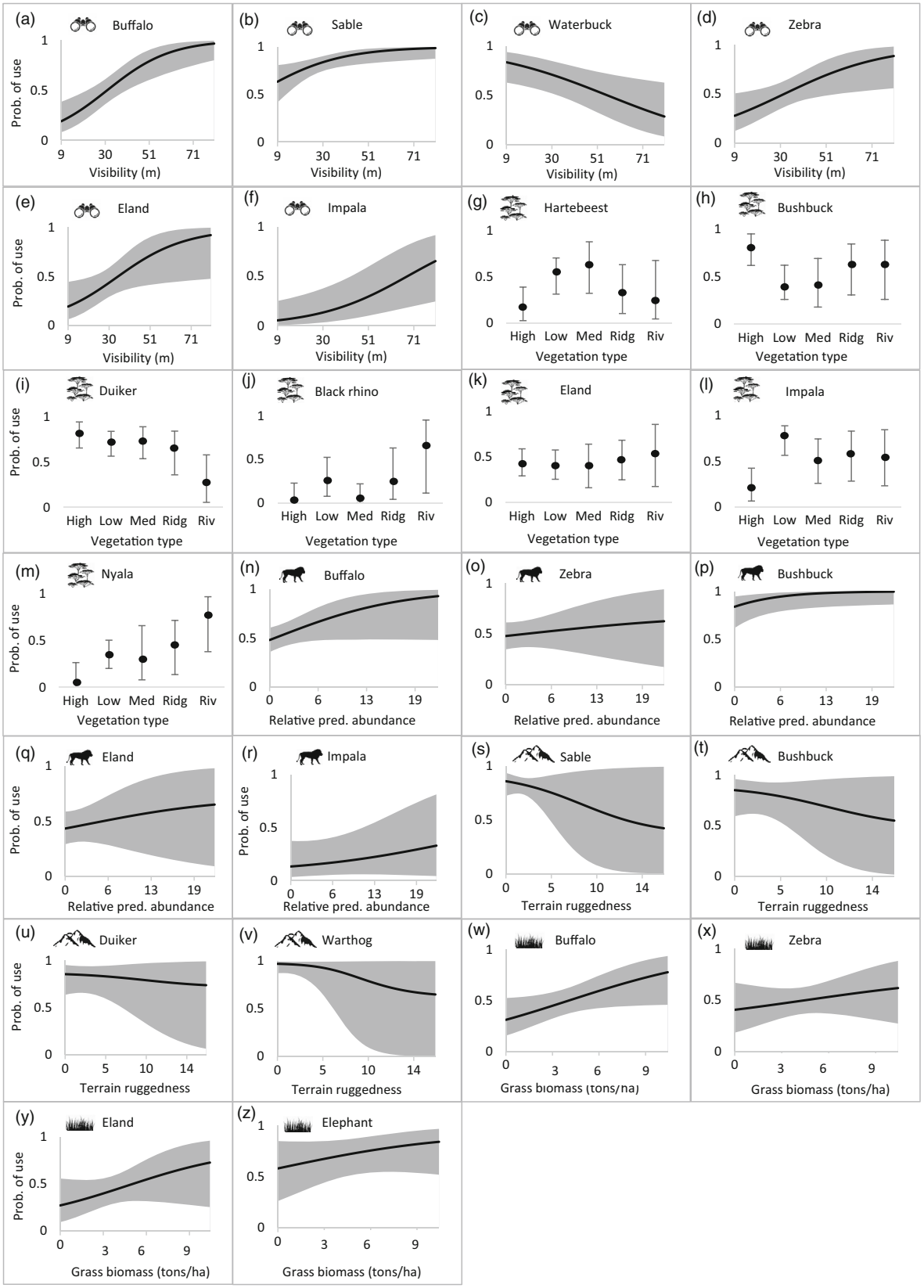

**Figure 4** Species-specific plots (a-z) of ecological covariates effect on ungulate space use (95% confidence intervals in grey). Only covariates from the plausible top models per species that influenced such a species space use by at least 10% over the full range of possible values for that parameter (See Table 1 for detail on each variable) are presented here, as they were considered to be truly informative (see text for more detail). The covariates are represented by the following symbols on each species-specific plot:  = Grass biomass,  = Relative predator abundance,  = Terrain ruggedness,  = Vegetation type,  = Visibility.

## Space use of ungulates in Majete

Kudu, warthog and sable are the most widely distributed species in Majete mirroring observations of kudu and warthog from the early 1980s (Bell, 1984). Following the widespread poaching that had decimated the herbivore populations, many species were re-introduced into Majete from 2003 onwards. However, kudu and warthog were not among those species, and managed to recover naturally to pre-poaching numbers suggesting some resilience to external threats in this environment (Chinomona et al., 2018; Hinde et al., 2001). Space use of kudu and warthog may thus not be the best species to monitor when external threat assessment is required, especially since naturally abundant species' space use varies little across a landscape once they start to reach high densities (Steenweg et al., 2017). Sable, a characteristic species of Miombo woodland (Frost, 1996; Hinde et al., 2001), had a widespread presence in Majete in the early 1980s (Bell, 1984) but needed to be re-introduced to reach a viable population size.

## Management-related predictors

Black rhinoceros, sable and zebra presence increased with distance from the fence, suggesting an avoidance of the reserve perimeter (Hayward & Kerley, 2009; Massey et al., 2014), likely due to anthropogenic-associated disturbance along the reserve boundary, such as agriculture and rural settlements. This avoidance reduces the effective reserve size for these species, a phenomena found in other studies (Rich et al., 2016; Woodroffe & Ginsberg, 1998). Avoidance of the fence line is especially concerning for rhinoceros, as they use high- and medium-altitude woodland significantly less than other vegetation types, which further limits their available space. Large-bodied herbivores are particularly sensitive to anthropogenic activities (Selier et al., 2015), with black rhinoceros similarly avoiding human disturbance in other small, fenced reserves (Odendaal-Holmes et al., 2014), as well as in larger, open landscapes (Gadiye & Koskei, 2016; Walpole et al., 2003) and zebra avoiding areas of human activity in Kenya (Young et al., 2005) and Namibia (Muntifering et al., 2019). The peculiar observation that bushbuck use areas closer to the fence more, may be an artefact of their avoidance of the medium-altitude vegetation that occurs in the centre of the reserve, rather than a preference for the fence line. Elephants have been found to avoid fences elsewhere (Selier et al., 2015), but which was not found in Majete.

Elephant, impala and warthog use of habitats close to roads, contrasts with other studies where they avoided roads due to human presence (Gaynor et al., 2018; Leblond et al., 2013; Mulero-Pázmány et al., 2016; Muposhi et al., 2016). Vehicle traffic on the majority of the roads in Majete is very low with lodges accommodating a maximum of 36 tourists per day (in 2018) and infrequent day visitors. Furthermore, tourism vehicles are restricted to the north eastern section (20% of the reserve) thus rendering the remainder of the reserve free from tourist vehicles. Mammals may thus be using roads in Majete as low resistance movement corridors as has been shown to be important for elephants when moving quickly between resource patches (Gaynor et al., 2018; Tsalyuk et al., 2019). It is also possible that water runoff from roads generate greener roadside vegetation luring herbivores to roads (Trombulak & Frissell, 2000; Tsalyuk et al., 2019), but we would then expect more species to be attracted to roads.

Zebra, elephant and hippopotamus's close association with water was not surprising given their known water dependence (Kihwele et al., 2020; Skinner & Chimimba, 2005). However, buffalo, also considered water dependent (Kihwele et al., 2020), were not limited by water proximity but rather associated with high grass biomass, suggesting a trade-off between surface water needs and food quantity during the dry season (Redfern et al., 2003). Distance to water might thus not be a reliable indicator of water dependency since herbivore distributions are confounded by other factors such as predation risk and food availability (Kihwele et al., 2020). Buffalo can travel as far as 15 km a day to reach water (Owen-Smith, 1996). Therefore, with less than 1% of Majete being more than 10 km from water it might also be that reliable surface water is readily available within Majete and limits its importance as a key predictor of space use. Intriguingly, the presence of water was not important for waterbuck space use. Smit et al. (2007) found that waterbuck prefer rivers over artificial waterholes, arguing that it is rather a preference for riparian vegetation than the avoidance of artificial waterholes. We found that waterbuck associated with areas of low visibility rather than water, supporting the view that vegetation in the vicinity of water rather than water availability may drive waterbuck space use.

Eland as a mixed feeder are generally considered to be water independent (Skinner & Chimimba, 2005; Taylor, 1969), but this is contested by our results, supporting the notion of Kihwele et al. (2020) that eland have medium water requirements. Interestingly though, warthog were not attracted to water despite being considered a water-dependent species (Kihwele et al., 2020). The same applies for black rhinoceros, which is surprising given findings in the Kruger National Park that black rhinoceros reduce their home range size and increase site fidelity during the dry season. However, Odendaal-Holmes et al. (2014) found black rhinoceros used areas closer to water less in the dry season, likely as a result of deteriorated habitat condition close to water and reduced browse.

Buffalo, bushbuck, elephant, hartebeest, impala and waterbuck frequented areas that seldom burnt more than areas subjected to frequent fires. Impala was also found to use unburnt areas more than recently burnt areas (Fig. 3t). A recent study in Majete restricted to the low-altitude deciduous woodland found that increased fire frequency results in decreased woody plant cover, height and stem diameters (Nieman et al., 2022), which supports the work of others in this biome (Frost, 1996; Furley et al., 2008; Ryan & Williams, 2011). Higher fire frequency was also associated with increases in the grass sward of less palatable short-statured increaser grasses (Nieman et al., 2022). In contrast to some of our results, Nieman et al. (2022) found that impala, kudu, buffalo, sable, waterbuck and zebra frequent areas that are burnt regularly. This contradicts our finding that impala, waterbuck and buffalo are more likely to be found in areas exposed to less frequent fires. Furthermore, Nieman et al. (2022) also found no evidence that elephant are affected by fire frequency, while our current study indicates a strong tendency for elephant to make use of seldomly burnt areas (Fig. 3k). These differences for certain species indicate that the way species respond to fires may be more complicated than originally thought and might also be scale dependant (Archibald et al., 2005) which was not considered in this study. Not only was the study of Nieman et al. (2022) conducted in a single habitat type, but it was also conducted during the wet season in contrast to our study's dry season focus. We therefore suggest that a more nuanced approach is needed to understand fire's affects on species which include habitat and seasonal differences.

## Ecological predictors

Buffalo, eland, elephant and zebra presence increased where grass biomass was high. As large herbivores with relatively low energy requirements, buffalo, eland, elephant and zebra feed unselectively, tolerating low quality forage but require it in large quantities to meet their nutritional needs (Hopcraft et al., 2010; Jarman, 1974; Owen-Smith, 1988). Eland is a mix feeder that consumes predominantly browse in the southern parts of Africa (Wallington et al., 2007; Watson & Owen-Smith, 2000), but are said to increase grass consumption further north and in East Africa (Cerling et al., 2003; Sponheimer et al., 2003).

Buffalo, eland, impala, sable and zebra were found to use areas with greater visibility more often. Only waterbuck had an affinity for areas with low visibility, corresponding with their aforementioned preference for dense riverine vegetation also seen in other studies (Owen-Smith, 1996; Smit et al., 2007). Greater grass height and vegetation cover are important for predator hunting success (Funston et al., 2001; Owen-Smith, 2019), so many species may use open areas as an anti-predator strategy (Funston et al., 2001; Hopcraft et al., 2005). Buffalo, eland and zebra used more open areas, but are not preferred prey species of lions in Majete (Briers-Louw & Leslie, 2020), possibly due to their success in avoiding lion predation by using the areas of higher visibility. Additionally, predation risk shapes the vigilance behaviour of zebra bachelor herds in Majete (de Vos et al., 2020), indicating that anti-predator strategies are important. Impala, a preferred leopard prey species in Majete (Briers-Louw & Leslie, 2020), may be using more open areas in Majete to avoid leopard habitat (i.e. habitat with intermediate cover; Balme et al., 2007). Surprisingly, the presence of bushbuck, also an important leopard prey item in Majete (Briers-Louw & Leslie, 2020), increases as predator relative abundance increases which may be driven by leopard selecting habitats that bushbuck use. Conversely, buffalo, eland and zebra are also positively associated with predator presence, although as previously mentioned, they probably avoid being killed in high numbers by using open areas (Briers-Louw & Leslie, 2020) and buffalo potentially also actively defend themselves (i.e. Tambling et al., 2015).

Sable, warthog, bushbuck and duiker are more readily found in easily negotiable terrain but the wide confidence intervals associated with space use in more rugged terrain suggest that they will utilise such areas if the area favours other important space use elements. Terrain ruggedness was also found to have an influence on ungulate space use in other African reserves (Davies et al., 2016).

The probability of different vegetation type use varied between species with much overlap between species for many vegetation types. Nyala, impala and black rhinoceros clearly use high-altitude Miombo woodland less than any other vegetation type, whereas bushbuck were commonly found here. Strong interspecific competitive interactions have been recorded between browsing bushbuck and the mixed feeding nyala, where nyala outcompeted bushbuck resulting in their spatial and temporal segregation (Ehlers Smith et al., 2020). Therefore, bushbuck may have resorted to using the high-altitude vegetation to avoid competition with nyala and impala. The high-altitude Miombo woodland has the lowest browse availability and habitat suitability for black rhinoceros in Majete (Gyöngyi & Elmeros, 2017), supporting the finding here that rhino use this vegetation the least.

## Management implications

The assessment of the patterns and predictors of ungulate space use at Majete provided insight on the functioning of this ecosystem, and may be useful for managers of other small, isolated, and fenced reserves, not only in the Miombo Woodland Ecoregion for which data are sparse, but also in other African savanna systems. Insight into vegetation type use by the different species can be used to inform carrying capacity estimates as it indicates the actual area used, while the effect that distance to water has on some species space use may be useful for artificial water point placement planning. However, it is clear that water dependence of ungulate species is a complex issue that is probably context specific, and we caution against generalisations across the African continent. Considering the high preponderance of anthropogenic land use adjacent to the reserve, the high historic levels of poaching and a low abundance of wildlife outside of reserves in Malawi (van Veldena et al., 2020), it is somewhat surprising that not more species avoid the reserve boundary. However, there are still parts

of the reserve that have some natural vegetation bordering it which possibly buffer the negative anthropogenic effect and effort must be made to retain these remaining pieces of intact land. Overall, ecological characteristics predominantly drive ungulate landscape use in Majete, indicating the critical importance of maintaining the natural interior characteristics of the reserve. The high value of Majete as an intact natural remnant within the region has been shown and our research highlights the need for similar studies in other isolated protected areas, which may be equally unique in their ability to conserve the biodiversity characteristics of the larger landscape.

## Acknowledgements

We are grateful to the Earthwatch Institute for funding this project, and for the many volunteers who assisted with fieldwork. We wish to thank African Parks (Majete) Pty Ltd. for supporting and permitting this study to be conducted in Majete, and for providing game scouts to assist with fieldwork. No research permits were needed as authority to conduct the research was granted by African Parks who manage the reserve. We are grateful to the three reviewers whose comments helped to improve the paper. This study was collaboratively conceived and designed by all authors. All authors read and approved the final paper. This work was supported by the Earthwatch Institute and a CPUT Mauerberger Foundation scholarship.

## Author contributions

All authors conceived the ideas and designed methodology; AL administered the project and acquired funding; SR collected the data; SR, CT and FR analysed the data; SR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Plots indicating the effect of covariates on buffalo space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S2.** Plots indicating the effect of covariates on hartebeest space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S3.** Plots indicating the effect of covariates on hippopotamus space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S4.** Plots indicating the effect of covariates on reedbuck space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S5.** Plots indicating the effect of covariates on warthog space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S6.** Plots indicating the effect of covariates on waterbuck space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S7.** Plots indicating the effect of covariates on zebra space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S8.** Plots indicating the effect of covariates on bushbuck space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S9.** Plots indicating the effect of covariates on duiker space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S10.** Plots indicating the effect of covariates on kudu space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S11.** Plots indicating the effect of covariates on black rhinoceros space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S12.** Plots indicating the effect of covariates on eland space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S13.** Plots indicating the effect of covariates on elephant space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Figure S14.** Plots indicating the effect of covariates on impala space use, whereby the covariates from the plausible top models are indicated, and which had a less than 10% influence on space use across the full range of possible values for that parameter (95% confidence intervals in grey), and were thus considered uninformative.

**Table S1.** The model combinations with an ΔAICc score of $< 2$ which were considered most likely to predict probability of use and detection.

**Appendix S1.** The variables used to predict detection probability and space use are listed with the methodology that was used to calculate either the categorical or continuous value for each variable to be used in the modelling process.