An Assessment of Mammal Diversity and Abundance in Makame Wildlife Management Area (WMA) by Camera Trap Survey

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Summary

A dry season camera trap survey was conducted in Makame Wildlife Management Area (WMA) from September to December 2017. The survey focused on an area of approximately 650 km^2 of dense Acacia-Commiphora thicket in the north of the WMA, which had been identified by Carbon Tanzania as an area of high biological interest. A total of 2,500 large mammals of 42 different species were recorded in 3,041 camera trap nights, giving a camera trap rate of 0.82. This trap rate is higher than the rates recorded using similar methods and equipment in both Tarangire National Park and Maswa Game Reserve. Two new species, Natal Red Duiker and Bushy-tailed Mongoose, were recorded for the WMA, and Fringe-eared Oryx were found to be common in the area. A total of 20 carnivore species were recorded, including African Wild Dog, an endangered species. This survey suggests that Makame WMA provides important habitat for multiple species of threatened mammals and hence is a very important area for large mammal conservation in the Tarangire ecosystem.

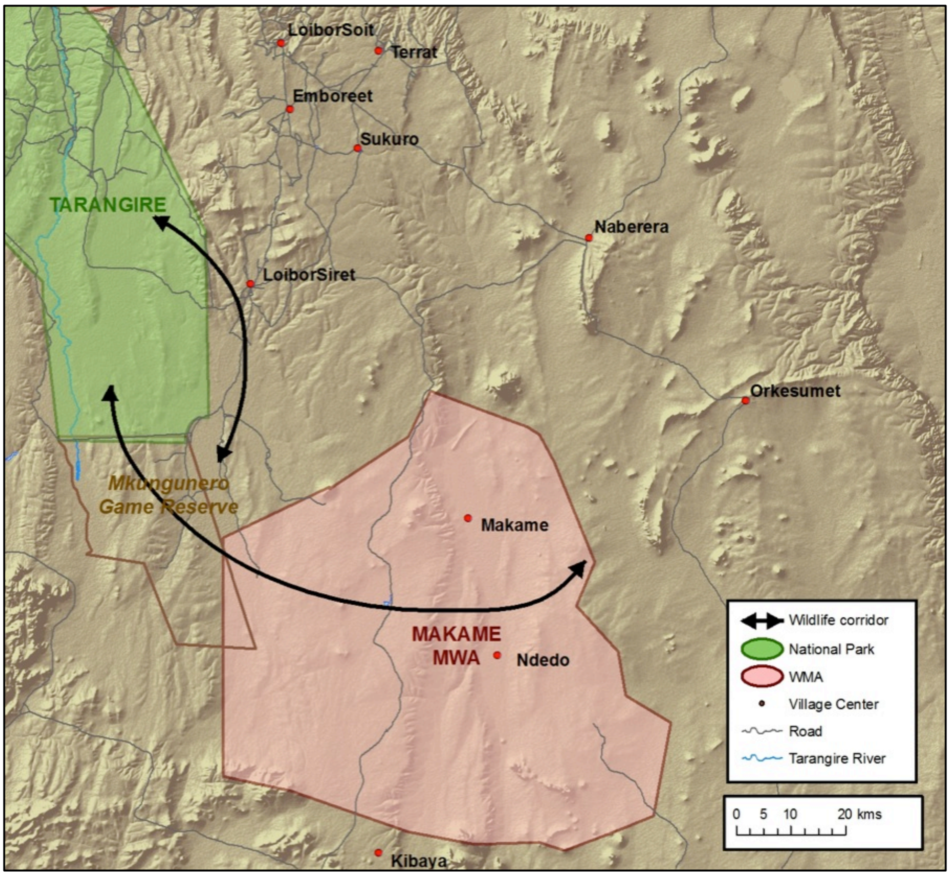
Introduction

The Makame Wildlife Management Area (WMA) lies to the south-east of Tarangire National Park, and is the largest community protected area in Tanzania. The WMA has a core area that covers 3,643 km^2, which has been set aside for wilderness and livestock, while a further 1,027 km^2 is village land established as a surrounding buffer zone for habitat, livelihood and subsistence use, including cultivation, fuelwood, livestock and sport hunting (Makame WMA RMZP 2017). The Makame WMA is made up of five villages (Irkiushiobor, Ndedo, Ngábolo, Katikati and Makame) with a total population of 14,854 people in 2012 (National Bureau of Statistics 2012). The communities are predominantly Masai, with pastoralism being the main livelihood for 93% of the households, although there is some cultivation (43% of households) concentrated around the village settlements. The WMA is also one of the oldest in the country, initially being established as a pilot WMA in 2002, before becoming a fully legalized entity in 2006.

The WMA is dominated by Acacia-Commiphora woodland and thickets with open grasslands in the seasonally-flooded lower lying areas. The landscape is interspersed with rocky hills and seasonal swamps creating diverse habitats that support both migratory and resident mammal and bird populations. Parts of the WMA are covered in extremely dense Acacia-Commiphora thicket that is almost impenetrable to humans, and which has never been properly surveyed before.

Wildlife in the Tarangire ecosystem is highly mobile. Most large ungulate populations exhibit large seasonal movements, dispersing widely during the wet season and concentrating around permanent water sources during the dry season. This movement is driven by variability in mineral content of the soils and the availability of standing water; the soil in Tarangire National Park is phosphorus-deficient, forcing the wildlife to move to the mineral and crude protein-rich plains on community lands outside the Park (Voeten 1999). Once the standing water in these dispersal areas dries up, the wildlife returns to the Park. There are several main wildlife corridors in the ecosystem that are used annually by migrating wildlife. The largest of the corridors is the southern migration corridor, that covers a vast area (see Figure 1) and the exact routes traversed by different species may vary annually (Foley and Foley 2014). The land directly to the south of Tarangire NP was designated as the Mkungunero Game Reserve in the early 2000s, and the southern corridor is believed to be the most ecologically intact of the major corridors in the ecosystem. A small population of wildebeest still migrates annually to Kimotorok during the wet season, although the number of animals using this area has declined significantly over the past 20 years. There is a resident sub-population of elephants (of approximately 400 individuals) that lives in the dense bushland in the Makame Depression that migrates to Tarangire National Park at the height of the dry season. Migration patterns of other species in this area are not well understood, although the Makame WMA is believed to support important populations of Gerenuk, Lesser Kudu, as well as a diversity of large carnivores that depend on this ungulate prey base, including a globally-important population of African Wild Dog (Foley and Foley 2014).

Figure 1: Migration routes from Tarangire National Park to the Makame Depression (based on zebra, wildebeest, and elephant movement data).



The Makame WMA was selected for intensive camera trap surveys for three reasons: 1) the area has a unique habitat type within the ecosystem, and has never been surveyed by cameras traps in the past; 2) previous ground work indicated likely high diversity of wildlife species, 3) the area is large, relatively intact, with low human impacts, and is a good distance from Tarangire National Park (>20km), suggesting it may have a different faunal composition.

Parts of Makame WMA are covered in extremely dense thicket, which makes it difficult to see and count mammal species in the area, particularly those associated with dense bushland. Even large mammals such as elephants and giraffe cannot be seen if they step a few meters off the road, resulting in very little information about mammalian diversity and density within the Makame area, although it was assumed to harbor important populations of thicket specialist species, such as Lesser kudu and African buffalo. In addition, small, nocturnal or crepuscular species are overlooked in ground count surveys; the unique habitat type associated with the Makame WMA suggested that it may contain species unique to the Tarangire ecosystem. Camera trap surveys offer a particularly suitable technique for recording wildlife in dense habitat including bushland and thicket, and its use has become increasingly common in wildlife studies (Ahumada et al. 2011; O'Connell et al. 2011, Bowkett et al. 2013).

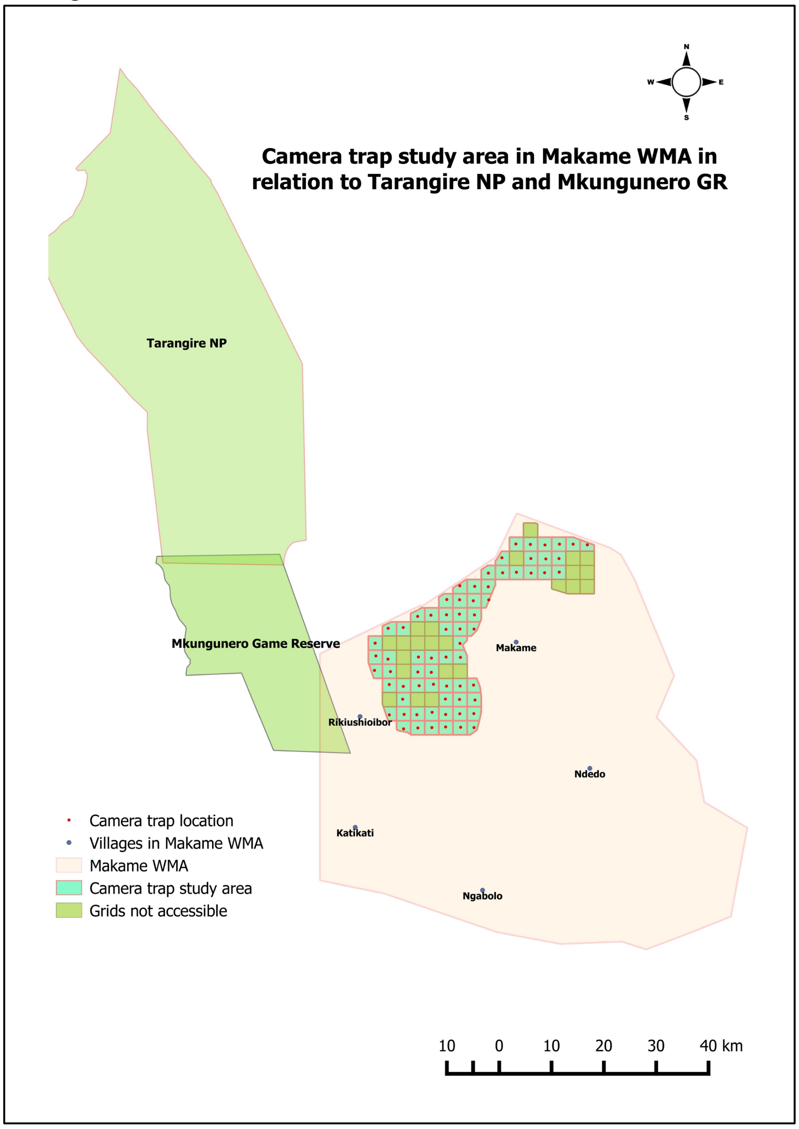
The camera trap survey set out to achieve three main goals:

a) To develop the first comprehensive mammal species list for the WMA,
b) To produce a baseline level of mammal abundance, occupancy, and association with anthropological variables that could be used by the WMA for comparison in future studies to assess the effectiveness of WMA management strategies,
c) To form part of a robust biodiversity baseline that Carbon Tanzania can incorporate into its project description document for the Verified Carbon Standard, which allows them to sell the carbon credits. This survey will be repeated by the WMA every five years as part of the monitoring plan.

Methods

An area of 652km^2 was surveyed within the Makame WMA (Figure 2). The survey area was selected after discussions with Carbon Tanzania to ensure overlap with their main area of interest within the WMA. This area was then reviewed for human activity using Google Earth, and approximately one-third was removed from the study area because of proximity to local settlements (known as bomas), which may have led to theft of the camera traps. The remaining area was divided into equal grid squares, each 2.7 km wide and covering an area of 7.3km^2. The survey area was split into a total of 92 grid squares, although 23 of these proved impossible to access in the field due to the dense vegetation, so a total of 69 grids were used in this survey, covering an area of 484 km^2.

Figure 2: Location of Makame Wildlife Management Area and the camera trap survey area, in relation to Tarangire National Park.



Camera traps were set in the middle of each grid, with Global Positioning System (GPS) receivers used to place each camera within 100 m of each central grid point. Cameras were usually attached to a tree or bush and positioned 30–40 cm above ground perpendicular to a game trail, in order to capture full body lateral photographs of mammals, to aid with identification. Vegetation type (thick bushland, thick woodland, open bushland and open woodland) was recorded during set up. The camera traps used in the survey were Reconyx HC500 HyperFire Semi-Covert IR digital cameras. Four of the cameras used white flash at night, while 61 cameras used infrared flash. The cameras were programed at high sensitivity with no delay, and set to take one picture per trigger. During camera set-up, the survey team triggered each camera while holding a white board on which was written the location ID, date and time. This was repeated upon camera recovery. A total of 49 cameras were set up between September 13 and November 2, 2017. Once those cameras had been taken down, a further 20 cameras were deployed between November 3 and December 19, 2017 to ensure that all grids were surveyed.

Wild.ID software (Tropical Ecology Assessment and Monitoring 2015) was used to extract Exchangeable Image File Format (EXIF) information from each photograph (including the name of the image, date, and time), and to organize the photographs of wild animals into events. Each 'event' was defined as a =>30 minute interval from the previous image sequence of that species. Therefore, if an animal was recorded multiple times during a 30-minute period, that event as recorded as a single sighting. The species in each photograph was identified and the data compiled into an Excel database.

Species distribution analysis

For the occupancy modelling, data were divided into five 10-day time intervals, with each interval treated as a replication. If a species was recorded at a camera trap during a specific time interval it was marked as '1', if it was not recorded it was marked as '0'. All occupancy modelling was conducted in PRESENCE 12.10 (Hines 2006). The resulting modelled occupancy figure is the portion of the survey area occupied by each species; essentially a modelled estimate of how widely distributed a species is across the survey area that takes account of the chance of non-detection of that species at a camera trap even though it may be present (i.e. a value of 1.0 means a species is found across all areas surveyed, a value of 0.5 indicates a species is found in half the survey area). Only those species recorded at six or more camera traps were included for the occupancy analysis in order to ensure reliability of model fit. The basic model, assuming constant probability across sites and across survey periods, was fitted to all species seen at six or more camera traps to generate estimates of occupancy. In addition, the naïve occupancy was calculated, which assumes detection is certain when a species is present, and is defined as the number of cameras where a species was recorded, divided by the total number of cameras. For species seen at eight or more camera traps, we also tested for the effects of four site-based covariates that were measures of anthropogenic impacts: the distance to the nearest boma (Distance boma); the total number of cattle photographed at that camera trap site over the survey (Cattle); the total number of people photographed at that camera trap site over the survey (Humans); and the distance to the Tarangire National Park boundary (Distance park). Models were run with each combination of these covariates. The distance estimates from the nearest boma and to Tarangire National Park were obtained using QGIS software (QGIS Development Team 2013). The final model selected was the most parsimonious model based on the Akaike Information Criterion (AIC). A model with a higher number of covariates was not selected over a model with a lower number of covariates unless ΔAIC >2 (Burnham & Anderson 2003).

Species diversity

The total number of ground dwelling mammals seen at each camera trap site provides a site-specific measure of species diversity. These measures were analyzed to assess overall species richness and to generate rarefaction curves using the package vegan (Oksanen et al. 2017) in RStudio (RStudio Team 2017). Rarefaction analysis allowed comparison of overall species richness between cameras sited close to the nearest boma (<6km) and those sited far away (>6km).

Species abundance

Indices of abundance were calculated using modelled occupancy (see above, Species distribution analysis) and relative abundance index (RAI). The RAI was calculated as the mean number of independent photographic 'events' per trap day x 100 (Amin 2015). Standard error for RAI was calculated as the standard deviation of the trapping rate divided by the square root of the number of trap days.

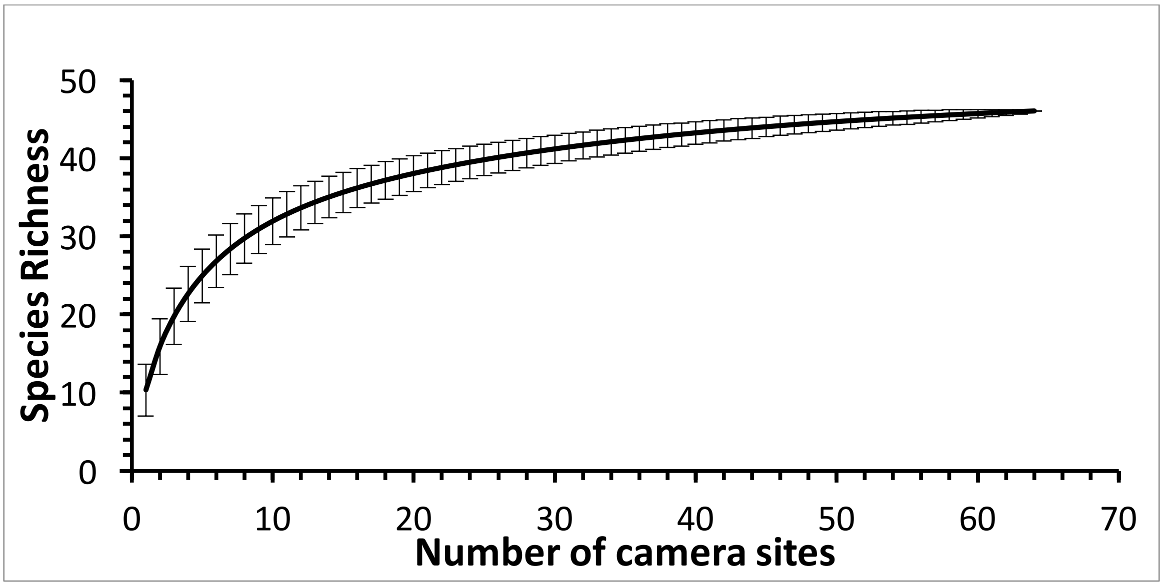
Results

The final sampling effort for the Makame survey was 3,041 camera-trap days, with camera trap days calculated as the total number of 24-hour periods in which each camera was operational. Three camera traps were stolen and one memory card was stolen.

Species composition

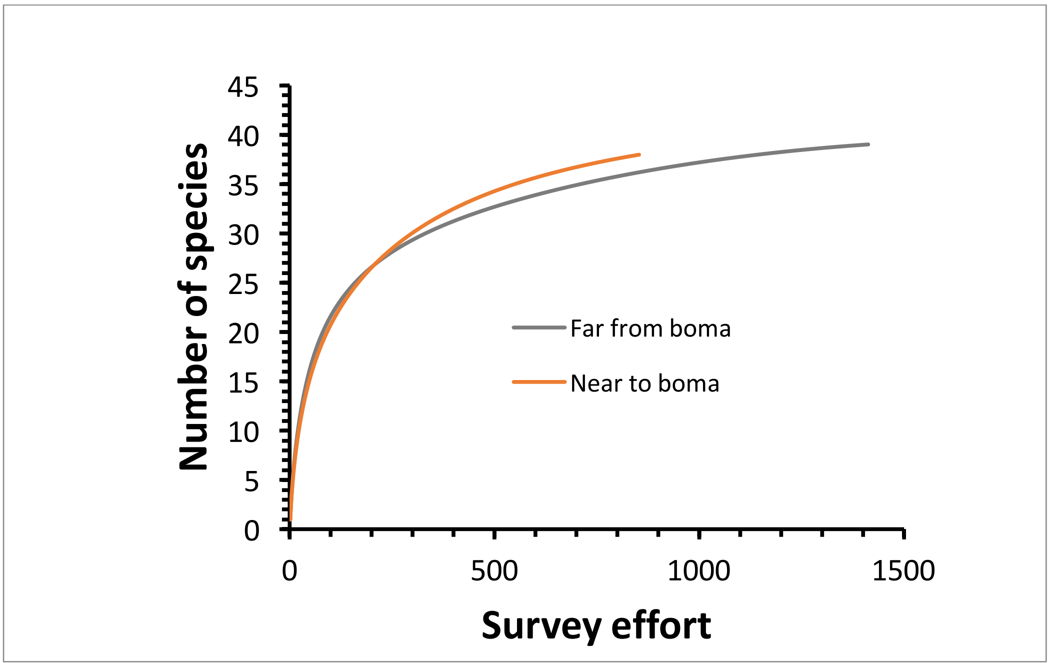
We recorded a total of 2,268 events and a total number of 2,500 aggregated photographs of 42 wild mammal species during the survey. The camera trap rate for the entire survey was 0.822. The species accumulation curve (Figure 3) shows a gradual levelling off with survey effort, which demonstrates that our camera trap design was sufficient to capture most species of ground dwelling mammal in the survey area. The total number of mammal species estimated as present in the survey area using the chao estimator is 48.5 (SE 2.9) and using the jacknife estimator is 50.9 (SE 2.2).

Figure 3. Species accumulation curve for all wild mammal species captured during camera trap surveys in Makame WMA



An average of 10.2 mammal species were detected at each camera trap site, but there was substantial variation between different sites (range 2-18). However, rarefaction analysis, which accounts for unequal survey effort (Sanders 1968), provided no evidence for substantial variation between species richness and distance to nearest boma (Figure 4). Both the steepness of the rarefaction curve and the overall asymptotes were very similar for camera traps sited close to bomas and those sited far away.

Figure 4. Rarefaction analysis for wild mammal species in Makame WMA by distance to boma.



Species abundance and distribution

Ungulates

A total of 17 ungulate species (including zebra and pigs) were recorded during the survey (Table 1). The most abundant species were Kirk's Dikdik (RAI = 1087, SE = 15.04), Lesser Kudu (RAI = 565, SE = 9.84) and Bush Duiker (RAI = 539, SE = 8.85), while Bushpig (RAI = 250, SE = 3.46), Giraffe (RAI = 218, SE = 3.18) and Impala (RAI = 343, SE = 7.58) were also frequently recorded. With the exception of the Giraffe, which is found across multiple habitat types, all of these species are bushland specialists. The first five of these species all had high modelled occupancies of > 0.7, indicating that they broadly distributed across the habitats surveyed. The Lesser Kudu, Bush Duiker and Bushpig are all uncommon or rare in Tarangire National Park and other parts of the Tarangire ecosystem, where the vegetation is typically much more open. The Makame thicket provides excellent habitat and is clearly a stronghold for these species in the ecosystem.

Table 1: Mammal species recorded in Makame WMA. Included for each species are (a) the number of camera trap events, (b) relative abundance index (RAI) with standard error, (c) the total number of animals recorded, (d) the modelled occupancy estimates, with 95% confidence interval range, and (f) naïve occupancy. Modelled occupancy was only undertaken for those species with captured at a minimum of six camera trap sites.

Species	Number camera trap events	Relative Abundance Index (RAI)	RAI Standard error	Total number animals recorded	Modelled occupancy	Modelled occupancy 95% CI range	Naïve occupancy
Kirk's Dikdik	674	1087	15.04	727	0.955	0.8639 - 0.9859	0.954
Lesser Kudu	305	565	9.84	335	0.858	0.7413 - 0.9277	0.831
Bush Duiker	264	539	8.85	266	0.745	0.5544 - 0.8722	0.754
Aardwolf	116	414	8.18	116	0.459	0.3358 - 0.5883	0.431
Bushpig	100	250	3.46	122	0.745	0.5544 - 0.8722	0.615
Giraffe	96	218	3.18	108	0.821	0.5915 - 0.9351	0.677
Impala	72	343	7.58	118	0.365	0.2449 - 0.5043	0.323
Spotted Hyaena	69	300	7.19	73	0.436	0.2895 - 0.5943	0.354
Common Warthog	68	213	3.71	74	0.694	0.4424 - 0.8658	0.492
Common Eland	64	256	2.62	68	0.479	0.3226 - 0.6390	0.385
White-tailed Mongoose	60	273	3.50	63	0.392	0.2639 - 0.5362	0.338
Aardvark	55	183	1.91	55	0.617	0.4121 - 0.7872	0.462
Crested Porcupine	46	209	2.37	48	0.397	0.2663 - 0.5447	0.338
African Elephant	28	233	3.12	38	0.245	0.056 - 0.404	0.185
Fringe-eared Oryx	26	217	4.08	29	0.275	0.1352 - 0.48	0.185

Species	Number camera trap events	Relative Abundance Index (RAI)	RAI Standard error	Total number animals recorded	Modelled occupancy	Modelled occupancy 95% CI range	Naïve occupancy
Leopard	25	208	2.25	26	0.231	0.1269 - 0.3827	0.185
Caracal	20	154	1.20	20	0.395	0.1494 - 0.7078	0.200
African Buffalo	17	170	1.92	28	0.162	0.0892 - 0.2773	0.154
Grant's Gazelle	16	533	8.18	32	NA	NA	0.046
Striped Hyaena	16	133	1.18	16	0.419	0.1255 - 0.7840	0.185
Common Genet	15	188	2.26	15	0.165	0.0753 - 0.3254	0.123
Honey Badger	15	125	0.82	16	0.567	0.0757 - 0.9544	0.185
Slender Mongoose	12	109	0.55	12	0.189	0.1058 - 0.3153	0.169
Scrub Hare	11	220	2.98	11	NA	NA	0.077
Bat-eared Fox	11	122	0.80	11	0.256	0.1324 - 0.4362	0.138
Greater Kudu	9	100	0.00	9	0.158	0.0820 - 0.2833	0.138
Vervet Monkey	8	200	1.48	9	NA	NA	0.062
Wild cat	8	133	1.48	8	0.173	0.0497 - 0.4560	0.092
Black-backed Jackal	6	100	0.00	7	0.106	0.0467 - 0.2211	0.092
Bushy-tailed Mongoose	5	250	1.28	5	NA	NA	0.031
Steenbok	5	125	0.91	5	NA	NA	0.062
Bushbuck	4	400	NA	4	NA	NA	0.015
Zorilla	4	133	1.05	4	NA	NA	0.046
Natal Red Duiker	3	300	NA	3	NA	NA	0.015
Large-spotted Genet	3	150	1.28	3	NA	NA	0.031
African Wild dog	3	100	0.00	7	NA	NA	0.046
African Civet	2	100	0.00	2	NA	NA	0.031
Lion	2	100	NA	2	NA	NA	0.031
Plains Zebra	2	100	NA	2	NA	NA	0.031
Banded Mongoose	1	100	NA	1	NA	NA	0.015
Coke's Hartebeest	1	100	NA	1	NA	NA	0.015
Dwarf Mongoose	1	100	NA	1	NA	NA	0.015
Cattle	118	562	13.72	565	NA	NA	0.323
Sheep and goats	2	200		20	NA	NA	0.015
Human	32	400	8.28	63	NA	NA	0.123

In terms of associations with anthropogenic variables, the Kirk's Dikdik and Lesser Kudu exhibited negative correlations with cattle and bomas, respectively, while Giraffe distribution was negatively correlated with both (Table 2). Impala, by contrast, were positively correlated with cattle, suggesting similar habitat use.

Surprisingly, the Fringe-eared Oryx was relatively abundant (RAI = 217, SE = 4.08) in the survey area, and was recorded at approximately 25% of the camera trap sites. This species is at the southern end of its global range in the Tarangire ecosystem, and numbers have declined over the past 20 years due to over-hunting (Foley and Foley 2014). Although Fringe-eared Oryx are found in both bushland and grassland, they usually avoid very dense thicket. The species has been recorded frequently in the open grasslands in central Makame, and the bushland part of the WMA clearly also forms an important habitat for this animal. This suggests that Makame WMA might form a more important stronghold for the Fringe-eared Oryx than previously thought. African Buffalo are another bushland species, but they were less commonly found than other bushland species (RAI = 170, SE = 1.92). Buffalo were positively correlated with cattle, suggesting similar habitat use within the WMA.

Table 2. Results from occupancy analyses for those species recorded at eight or more camera traps. Occupancy was analyzed against four anthropogenic variables: (1) distance to nearest boma, (2) distance to Tarangire National Park, (3) total number of cattle recorded at each camera trap site, (4) and total number of humans recorded at each camera trap site. The best model, according to the AIC, is reported in the table. In a few situations not all variables could be included because of problems of model convergence.

Species	Best model	Covariates	Positive correlation	Negative correlation	AIC
Kirk's Dikdik	Cattle	-0.0415		Cattle	379.53
Lesser Kudu	Distance-boma	0.4209		Bomas	422.65
Giraffe	Distance-boma, Cattle	0.5995, -0.0603		Bomas, cattle	343.35
Bush duiker	Basic model	-			409.43
Bush pig	Basic model	-			340.31
Common warthog	Basic model	-			276.98
Aardvark	Basic model	-			270.19
Honey badger	Humans	0.4474	Humans		115.72
Common eland	Basic model	-			244.10
Aardwolf	Basic model	-			283.10
Spotted hyena	Basic model	-			230.63
Striped hyena	Distance-boma, Cattle, Humans	0.67, -0.57, 3.48	Humans	Bomas, Cattle	113.30
Crested porcupine	Basic model	-			227.58
Caracal	Distance-boma	-0.864		Bomas	132.36
White-tailed mongoose	Basic model	-			228.93
Species	**Best model**	**Covariates**	**Positive correlation**	**Negative correlation**	**AIC**

Impala	Cattle	0.092	Cattle		213.07
Fringe-eared oryx	Basic model	-			132.92
Savanna elephant	Cattle, Humans	-0.07876, 0.4745	Humans	Cattle	132.28
Leopard	Distance-boma, Humans	0.389772, 1.425810	Humans	Bomas	126.16
Slender mongoose	Basic model				136.72
African buffalo	Cattle	0.02318	Cattle		125.31
Greater kudu	Cattle	-26.6955		Cattle	108.95
Bat-eared Fox	Distance-park	0.2255		Park	83.76

An important finding of the Makame survey was the first record of the Natal Red Duiker for this area. This species had not been recorded either from Makame WMA or Tarangire National Park before, although there had been sporadic records from hunters from areas of dense bushland in the southern Masailand (Foley et al 2014). Their distribution in Masailand, and in Makame WMA is likely to be limited by their need for access to permanent water. The Natal Red Duiker was recorded at a single grid, and the three photos may have been of the same individual, suggesting that the species is rare in the WMA. The nearest known population where this species is locally common is in the Ufiome forest near Babati to the west of Tarangire National Park.

Carnivores

This survey recorded 20 carnivore species, suggesting a rich carnivore assemblage. The most abundant carnivore in Makame WMA is the Aardwolf, a small hyaeanid that feeds on termites. This species was recorded at 28 of the 65 stations with an RAI of 414 (SE 8.18). The camera trap rate for Aardwolfs in this survey (calculated as the number of camera trap sightings divided by the number of camera trap nights) was 0.38. A camera trap survey using the same method and model of camera traps conducted during the dry season of 2008 both within Tarangire NP and in the surrounding pastoral areas in the Simanjiro (Msuha 2009), recorded a camera trap rate of 0.0019 from Tarangire NP and 0.0076 from the pastoral areas respectively. This suggests that abundance figures in Makame are almost 50x higher than in other parts of the ecosystem, which is probably linked to the greater availability of termite species, which form its main prey, particularly *Trinervitermis bettonianus*.

Both Spotted and Striped Hyaenas were recorded in the area, and while the occupancy model suggested that both share approximately the same distribution (Spotted Hyaena occupancy = 0.436, Striped Hyaena = 0.419), the Spotted was more abundant (RAI = 300, SE 7.19) than the

Striped (RAI = 133, SE 1.18). The Spotted Hyaena did not exhibit any correlation with anthropological variable, while the Striped Hyeana avoided humans, but was positively associated with both cattle and bomas. This species is a scavenger that frequently feeds on human refuse.

There were 25 camera trap records of Leopards during the survey, with a modelled occupancy of 0.23. Leopards were found to be positively associated with humans, although they were more common further away from bomas. Associations between people and Leopards have been found by other studies (e.g. Wang and Macdonald 2009); in Makame WMA our results suggest that Leopards may avoid areas of permanent habitation, such as bomas, but may be attracted to areas of occasional human use, as indicated by records of humans in camera traps. The Honey Badger was another species that showed a positive correlation with humans in the WMA. This is a very versatile species that scavenges on human refuse and is one of the few mustelids that appears to show little fear of humans. Honey Badgers are widely distributed across the WMA, with an estimated modelled occupancy of 0.57. The African Wild Dog is a globally endangered species (IUCN 2012), which was recorded during the survey. There were three Wild Dog records, with a total of seven individuals, recorded at three different grids.

The survey recorded five sightings of Bushy-tailed Mongoose at two different grids. This is a new record for the WMA, and only the second record for the southern half of the Tarangire ecosystem. The Bushy-tailed Mongoose was originally thought to be rare across East Africa, with very few records from the region (Taylor 1987). However, camera trap surveys have shown that it is widely associated with dense vegetation across Tanzania (Foley et al. 2014), and there are now records for urban areas including Arusha. This species was probably overlooked as it is strictly nocturnal, and likely confused with the similar looking Marsh Mongoose. The increase in the use of camera traps as a survey tool has greatly improved knowledge of this species in Tanzania.

Afrotheria

The African Elephant was relatively abundant (RAI = 233, SE = 3.12) in the MWA. There is a resident population of approximately 400 elephants that live in the dense thickets of Makame WMA for most of the year while the waterholes in the area have water, and then migrate to the southern section (Mkungunero) of Tarangire National Park during the dry season. This survey was conducted at the height of the dry season, which suggests that some elephants remain in the WMA throughout the year. Elephants are obligate drinkers, indicating that they must be accessing water from somewhere in the WMA or nearby areas. All of the waterholes visited during the first phase of the camera trap set-up in September were dry, so it is not clear where the elephants were drinking. Occupancy modelling showed a negative association between Elephant and cattle records, suggesting that elephants avoid cattle grazing areas. However, the model also showed a positive association between Elephant presence and records of humans in camera traps within the WMA, although the reasons for this are not clear. The Aardvark was both common (RAI = 183, SE = 1.91) and well distributed (0.617) across the Makame WMA. Like the Aardwolf, this species is also a specialist termite (and ant) feeder, and is likely to therefore also benefit from the high density of termite mounds found in the WMA.

Discussion

This study has demonstrated that Makame WMA has a high diversity and density of large mammals, and should be considered a very important area for mammal conservation within the Tarangire ecosystem. When compared with the results of two other camera trap surveys, both in protected areas, that were carried out by TAWIRI staff using the same camera trap model and methodology, the figures for the Makame survey are surprisingly high. The camera trap rate (the total number of animals sighted / total trap nights) for Makame was 0.82 (2,500 sightings, 3,041 trap nights), with 42 species recorded. A study conducted in the dry season in Tarangire National Park in 2007 had a trap rate of 0.79 (2,965 sightings, 3,699 trap nights) and recorded 35 mammal species, while a survey in Maswa Game Reserve to the west of the Serengeti National Park, had a trap rate of 0.69 (5,697 sightings, 8,256 trap nights) and recorded a total of 49 species.

The occupancy modelling approach allowed the examination of species occupancy against a number of potentially important anthropogenic covariates. Those species where there was model convergence, and hence where we can be reasonably confident of the results, broadly fell into four categories: 1) those that showed negative associations with measures of anthropogenic impacts; 2) those that showed positive associations; 3) those that showed a combination of positive and negative associations; and 4) those that showed no associations. Species showing negative associations included Dik dik; Lesser Kudu; Giraffe; Caracal; Greater Kudu; and Bat-eared fox. The ungulates in this list browse in thick thickets which tend to be less common close to bomas and the grassland areas which tend to be preferred pasture for people and their cattle. It is unclear why Caracal and Bat-eared Fox show a negative association. Caracal showed an increasing occupancy with distance to the nearest boma. Bat-eared Fox showed decreasing occupancy with distance to the park. It is possible that some aspect of the diet of these species declines with human impacts.

Those species showing a positive association with measures of anthropogenic impacts, included Honey Badger; Impala; and Buffalo. Both Impala and Buffalo showed a positive association with the number of cattle photographed at the site. Impala may derive grazing facilitation benefits from the presence of cattle, while Buffalo are attracted to the prime cattle grazing areas where they likely compete with cattle for similar forage (Fynn et al. 2016). Honey Badger was positively associated with the number of humans recorded at sites. This species often follows people, or vice versa, due to their joint predilection for honey.

Those species showing a combination of positive and negative associations included striped hyena, elephant and leopard. Striped hyena occupancy was positively associated with the records of humans photographed at a site, while negatively associated with bomas and cattle. This is a species which often scavenges from humans and hence might be expected to benefit from the presence of humans, thus a positive association with human presence at camera trap sites is not surprising, but a negative association with bomas is unexpected. Striped hyenas can be persecuted, as people often do not distinguish the species from spotted hyenas (the latter of which is a common predator of livestock), and this might explain these observations. Both Elephants and Leopards were positively associated with humans, and negatively associated with cattle. This is possibly related to the presence of people collecting honey, building material and hunting illegally in parts of the WMA. The remaining species either showed no association with any of the measured anthropogenic impacts, or there were problems in model convergence.

When interpreting these survey results, however, it should be remembered that those grid squares with the highest anthropogenic impact (amounting to approximately one third of the total) were not included in the survey because of the high risk of theft of the camera traps. This was done because the principle goal of the study was to develop a comprehensive species list for the WMA, and the camera traps were positioned accordingly. Thus the results need to be interpreted with caution, as the grid squares surveyed have lower anthropogenic impacts than average, and may thus show biases in measures of species diversity and occupancy. Some of the associations with anthropogenic impacts may increase or decrease if a wider range of anthropogenic impacts were to be included. Thus, in particular, those species showing no association between occupancy and the range of human impacts covered here, may start to show associations should the range of those human impacts be increased. Nonetheless, despite these provisos, two thirds of grid squares were eligible, thus the diversity recorded and the results observed is unlikely to be completely atypical of the survey area. It is also important to note that, particularly where species are seen infrequently, there may not be sufficient power in the current analyses for detection anthropogenic impacts in our models.

Although Makame WMA is a multi-use area with little anti-poaching presence, the large area of dense thicket and bushland appear to act as a refuge for mammals. Access to many of the grids is extremely difficult by vehicle, and parts of the thicket are completely impenetrable to vehicles, and, in some areas, to people on foot. This creates a safe area where mammal species can thrive. The fact that the area still supports a relatively large resident population of African elephants with very little protection indicates the importance of the thicket as a barrier to poaching. However, while the dense nature of the northern thickets provides protection for large mammals, this is not the case across other parts of the WMA, and evidence collected during the survey revealed that poaching levels in general within the WMA are high. The team recorded poached carcasses of Giraffe, African Buffalo and Common Eland within the WMA, as well as four old Elephant carcasses. It appears that most of the poaching incidences are occurring near waterholes, where the poachers build temporary platforms in trees and lie in wait for the animals. One camera recorded photos of five motorbikes with a total of nine poachers, carrying large loads (probably of dried meat), guns and dead guineafowl. As a result of this survey, TANAPA[1] and the KDU[1] carried out an anti-poaching sweep across the WMA, which led to the arrest of a number of poachers and the confiscation of their equipment. However, in the long run, it is important that wildlife monitoring surveys such as this are repeated while capacity for effective anti-poaching measures is developed and supported within the WMA to allow effective long term monitoring and a permanent and rapid response to poaching incidences.

The vegetation structure of the Makame WMA provides habitat for bushland specialists that are less common or absent from other parts of the ecosystem. Lesser Kudu, Bush Duiker, Bushpig, Aardwolf, Aardvark and Caracal are all relatively abundant in the WMA. Additionally, two bushland dependent species that were formerly not known from the WMA, the Natal Red Duiker and the Bushy-tailed Mongoose, were recorded in small numbers during the survey. An unexpected finding was the relatively high abundance of Fringe-eared Oryx in the WMA. This

[1] Tanzania National Parks Authority (TANAPA) and Wildlife Division Anti-poaching Unit (KDU)

species typically migrates large distances within the ecosystem, and most populations occur outside Tarangire NP, making them particularly vulnerable to illegal hunting. As a result, their numbers have greatly declined in the past 20 years and they are now rare across most of the Tarangire ecosystem (Foley and Foley 2014). This survey suggests that the dense bushland in the north of the WMA might serve as an important refuge for this species in the area. Makame WMA also harbors resident populations of the endangered African Wild Dog. Although this survey produced only three records for this species, the local communities suggest that the thickets provide regular denning sites for the Wild Dogs. With access to safe denning sites, relatively low Lion numbers (Lions are important predators of Wild Dogs, Woodroffe and Sillero-Zubiri 2012), and large area of low human density, Makame WMA may prove to be an important site for this species. One unexpected omission from the survey's mammal list was the Gerenuk, which is a common species in the WMA. However, while the Gerenuk is closely associated with Acacia woodland in the area, this survey suggests that it avoids the areas of denser vegetation.

It is unclear whether the majority of mammals using the thicket are resident individuals or if there is a seasonal influx of migrating species from Tarangire National Park during the wet season. The Elephant population in the area is known to migrate and abundance estimates would be expected to be higher in the wet season. African Buffalo movement patterns in this part of the ecosystem are not known, although they are also seasonal dispersers from the Park, and their numbers are also likely to increase during wetter times of the year. It would be useful to learn more about the seasonal movements of the large mammals using this area, although unfortunately the logistics of setting up the camera traps in the wet season are formidable, as access is exceedingly difficult. This could be achieved by placing the cameras shortly before the rains, when access is still feasible, and leaving them with the cameras set to battery-saving mode throughout the wet season until they can be collected again. This would also hopefully provide information on whether the thicket serves as a calving area for wildlife in the WMA.

All evidence from this survey suggests that the area of dense thicket in northern Makame WMA is of high importance for large mammal conservation and should be prioritized for protection and management by the WMA.

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Appendix: Selected camera trap pictures from the Makame WMA survey

Figure 1. Aardvark

Figure 2. Female African elephant and young calf.

Figure 3. Male Lesser kudu

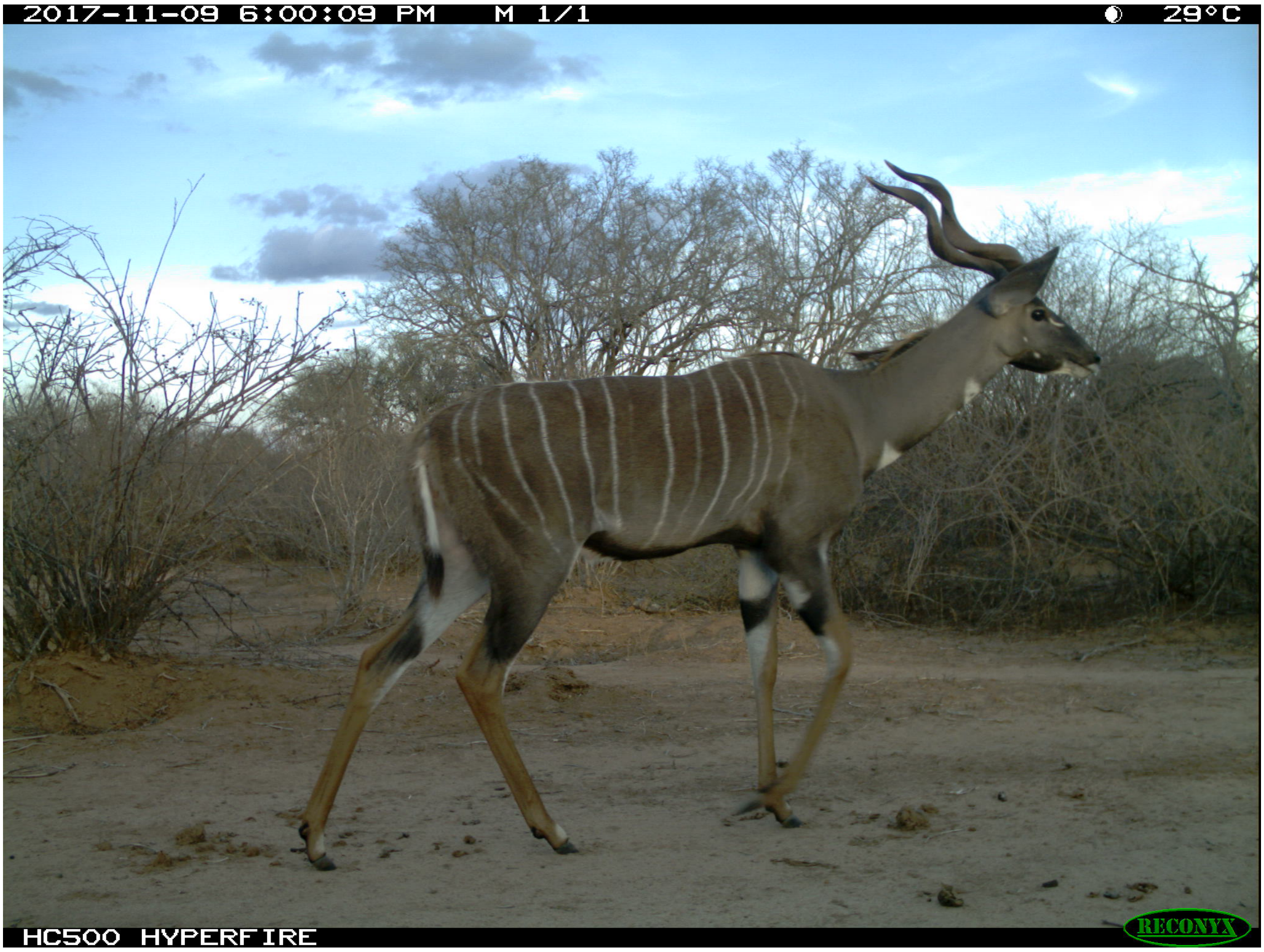

Figure 4. Male Fringe-eared oryx

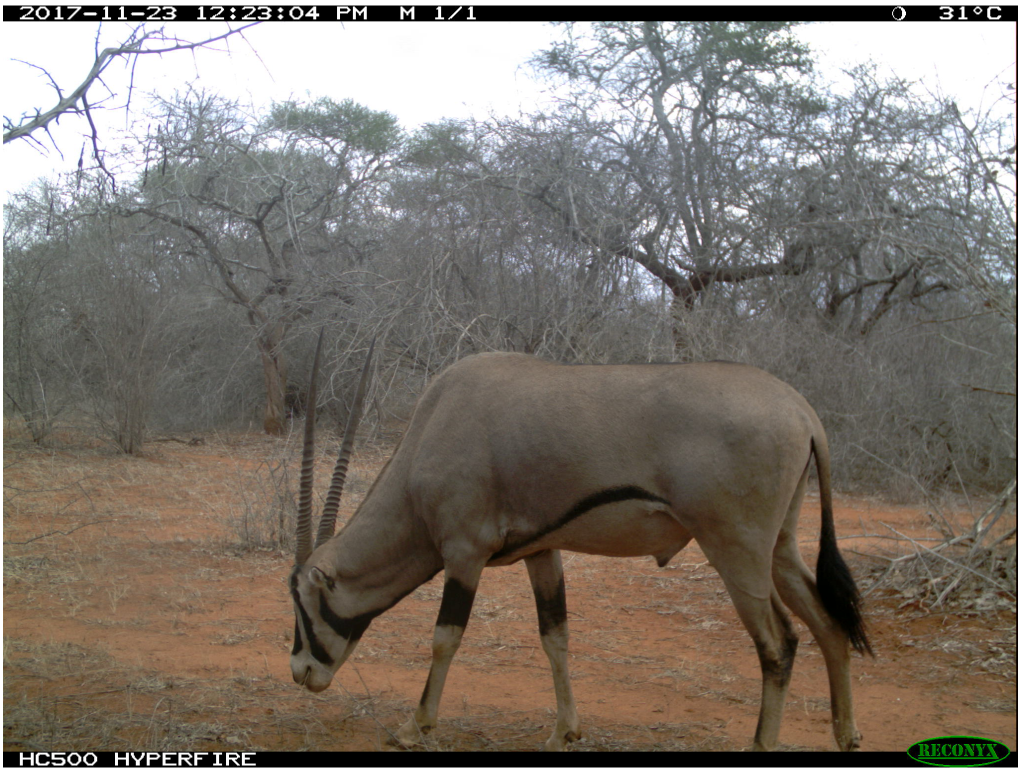

Figure 5. Bush duiker

Figure 6. Natal red duiker

Figure 7. Aardwolf

Figure 8. Striped hyaena

Figure 9. Bushy-tailed mongoose

Figure 10. Caracal

Figure 11. African wild dog

Figure 12. Bushpig family