Differential Effects of Fire on Small Mammal Communities in the Busanga Flood Plain, Zambia

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Abstract

We assessed effects of vegetation and fire on small mammals in open vegetation formations of the Busanga Flood Plain (Kafue National Park, Zambia) in areas of low and high fire recurrence. The impact of fire was related further to the time elapsed between the last fire and the time of trapping (fire age). Sampling sites covered three management zones: intensive utilization (tourist areas), wild (less used), and wilderness (no road access). Vegetation type, fire recurrence, fire age, and management zone were independent variables. Communities were similar in grassland and on termitaria but differed from miombo. Species richness was highest on termitaria, followed by grassland and miombo. Species numbers declined with increasing fire frequency but were unaffected by fire age. In contrast, the average body mass of species occurring at any one site (only adult individuals considered) declined with the time elapsed between the time of capture and the last fire (the longer the time interval, the lower the body mass of species averaged over the species found at the site). This response implies higher vulnerability of the smaller species to fire and slower recolonization potential of smaller species after fire. The interactions between fire, vegetation characteristics, and small mammals need to be reviewed, given their importance in the functionality of this ecosystem.

Fire is an integral part of African savannah ecosystems (Green, Roloff, Heath, & Holekamp, 2015; Parr & Chowan, 2003; Plasvic, 2014; Salvatori, Egunyu, Skidmore, de Leeuw, & van Gills, 2001; Swanepoel, 1981). In concert with grazing by large herbivores, it determines the physiognomy of large tracts of land. Apart from being a natural phenomenon, fire is widely used as a management tool in protected areas in Africa. The purpose of its use ranges from clearing vegetation for photographic tourism to fostering pastures for wildlife (Chanda, 2007; Green et al., 2015; Kampamba, Chansa, & Changwe, 2005; Parr & Chowan, 2003). In the Kafue National Park (KNP), Zambia, fire is predominately used during the early dry season (May to mid-July) as a means of reducing the probability of catastrophic fires, and to improve visibility for tourists to view and photograph game. Fires are set along the boundaries, access roads and fire breaks. Other management objectives for fire include: inducing fresh forage flush for wildlife grazing, fostering natural succession of fire sensitive vegetation, reducing soil erosion in the event of late season fires, and controlling insect pests (Chanda,

2007; National Parks and Wildlife Services/Japan International Cooperation Agency [NPWS/JICA], 1999).

Whilst most early fires are started by management, unplanned fires at any time of the year outnumber them (Chanda, 2007). These were earlier thought to originate from local communities in the Open and Game Management Areas bordering KNP (Chanda, 2007), but recent evidence alludes to fires beginning and occurring more frequently in the park as opposed to the Game

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Management Areas or open areas (Kelly, 2014). In fact, the park has the largest proportion of areas with high fire recurrence (Figure 1) even in critical habitats such as the Busanga Flood Plain.

Given the size of KNP ($\sim$22,400 km^2) and the lean resources available to manage it, (NPWS/JICA, 1999; Zambia Wildlife Authority [ZAWA], 2011) unplanned fires remain a major challenge to conservation. Most of the Park's rangeland is burnt annually, despite the prescribed rest interval of 2 to 3 years in its fire management plan. Furthermore, early burning as per current practice does not favor all wildlands. For instance in areas such as the Busanga Flood Plain (predominately a grassland), early fires are thought to interfere with processes such as rooting, seeding, and seed dispersal for grasses (Moss, 1973). The extent of interference is thought to directly depend on the amount of rainfall received. In a wet year ($>$1,000 mm), most areas remain moist till the mid dry season (July to August), thereby inhibiting the spread of early fires. The rainy season in Zambia ends in April and paves way for the dry season which begins in May and lasts to early November (ZAWA, 2011).

Very little is known about the influence of the current fire regime on biodiversity in KNP (Kinahan, 2003). Stakeholders speculate on a significant alteration in the vegetation structure that would result in reduced fodder and cover for species (Parr & Chowan, 2003). Small mammals are a matter of concern, as faunal studies in KNP tend to focus on larger species (ZAWA, 2005). Yet, small mammals (rodents and shrews) play a cardinal role in ecosystem functionality. They occur at several trophic levels, consuming substantial amounts of plant material, insects, and arthropods; serve as prey; and are important for perturbation of the soil (MacFadyen, Avenant, van der Merwe, & Bredenkamp, 2012; Timbuka & Kabigumila, 2006).

While several studies demonstrated the impact of fire and vegetation cover on small mammal communities, the evidence for fire effects is inconsistent. Some authors have described fire as having little impact on small mammal diversity, unless coupled with grazing (Salvatori et al., 2001) and rainfall (Yarnell, Scott, Chimimba, & Metacalfe, 2007). Others describe its effects as short lived and associated with the removal
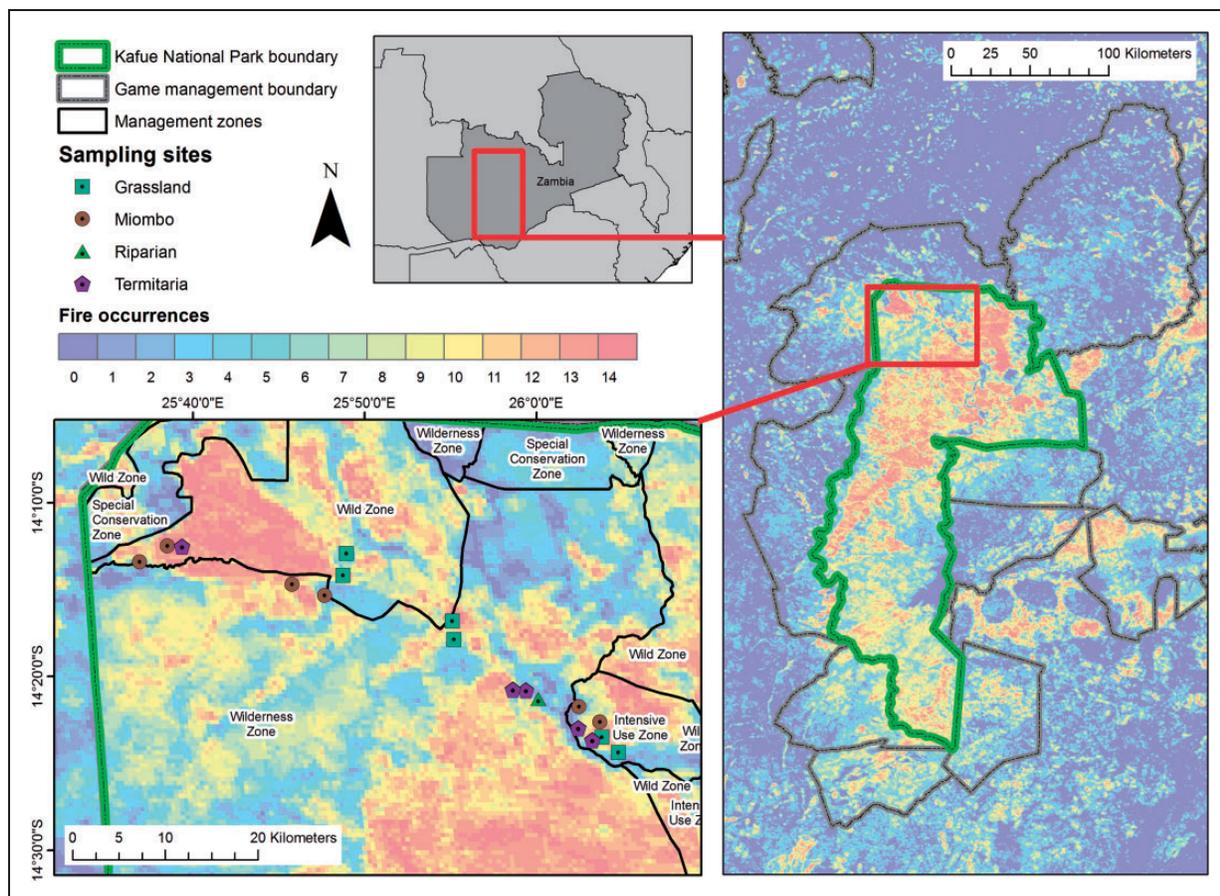

Figure 1. Sampling sites depicting the vegetation, fire recurrence, and management zones in the Busanga Flood Plain, north–west of Kafue National Park. Fire occurrences indicate the number of years with fire between 2000 and 2013 (base map from Kelly, 2014).

of vegetation cover (Plavsic, 2014; Swanepoel, 1981). Yet others describe it as having a positive impact on small mammal diversity, as species diversity is higher in areas where fire is a periodic disturbance (Bowland & Perrin, 1993). In the drier savanna regions (Kalahari savannah rangelands), species richness and abundances of small mammals had been negatively affected by shrub encroachment, brought about by overgrazing (Blaum, Rossmanith, & Jeltsch, 2006), though grazing itself had no significant impact (Bösing, Haarmeyer, Dengler, Ganzhorn, & Schmiedel, 2014).

Similar to the situation described for grazing, fire as a single factor didn't have a direct impact on small mammals (Swanepoel, 1981; Yarnell et al., 2007) but acted through the animals' response to reduced cover to emigrate or avert predation. Diurnal species seem to be more affected by the removal of vegetation cover as nocturnal species, as the former would be more prone to predation than the nocturnal species, whose predators rely on hearing or smell to detect prey (Hauptfleisch & Avenant, 2015; Joubert & Ryan, 1999). For the time being, it seems premature to try synthesizing these disconnected results, as the different studies consider different environmental drivers in different combinations and have been carried out in different regions. Yet, they provide the basis and framework to add on to.

Ecological studies and community comparisons between sites are often hampered by taxonomic issues, such as different species compositions or taxonomic uncertainties that make comparisons difficult. Functional and life history traits can be used to replace species names and thus replace site specific taxonomies by generalizable characteristics that facilitate comparisons between sites (Fox, 2011; Violle et al., 2007). As illustrated by the different predation risk of diurnal versus nocturnal species (Hauptfleisch & Avenant, 2015; Joubert & Ryan, 1999), the survival or persistence of species after disturbances of their habitat can often be linked to its life history or functional traits (Plavsic, 2014). Since body mass shows allometric relationships to a large number of life history traits (e.g., mobility, home range size, resistance to variation, and reproductive traits), it can be used as a proxy for life history traits that are favorable or unfavorable under different disturbance regimes (e.g., Brown, 1984; Stearns, 1992).

In order to fill some of the gaps in our knowledge of small mammal interactions with vegetation formations and ambient conditions, we addressed the following questions:

(i) What are the effects of vegetation types, fire recurrence, and the time since the last fire (fire age) on the taxonomic composition and similarity of small mammal communities in the Busanga Flood Plain?
(ii) What are the effects of vegetation types, fire recurrence, and fire age on the species richness of small mammals in different communities in the Busanga Flood Plain?
(iii) What are the effects of vegetation types, fire recurrence, and fire age on body mass and functional traits of small mammal communities in the Busanga Flood Plain?

Method

Study Area

The Busanga Flood Plain is located between about 25° 25' E/13° 45' S to 26° 10' E/14° 25' S and covers some 750 km^2 (NPWS/JICA, 1999). It is a wetland of international importance listed as Ramsar site no. 1659 of the Ramsar Convention of Wetlands of International Importance (Information sheet on Ramsar Wetlands [RIS], 2002). It is principally drained by the Lufupa River that constitutes the middle catchment area of the Kafue river basin (RIS, 2002). This basin is the largest subbasin of the Zambezi River (156,995 km^2) and lies entirely within Zambia. The Kafue Basin is often described as the lifeline for most of Zambia (ZAWA, 2011), as it is the main provider of water for major cities and most of Zambia's wildlife estate. Annual rainfall is around 1,100 mm and begins to fall in November, ending in April the following year. The dry season (May to November) is divided into two season; cool, dry (May to August), and hot, dry (Septemberto November; ZAWA, 2011).

Trapping Sites

Trapping sites where categorized based on vegetation type, management zone, fire regime, and fire age (Table 1). These characteristics were used as independent variables in the analyses. Based on the vegetation descriptions by Mwima (2006), management zones (NPWS/JICA, 1999), and fire recurrence (Kelly, 2014), 17 sampling sites were established by stratified random assignments. The initial intention was to achieve a balanced design of capture sites for the vegetation types of grassland, termitaria, and miombo forest. Since we could not find a termitaria site with low fire recurrence in the wild zone, we achieved only an unbalanced design for termitaria. Sites could not be stratified systematically with respect to fire age.

Data Collection

All data were collected during the dry seasons (August to October) of 2014 and 2015. Wet season captures were not possible as the Busanga Flood Plain is flooded during the wet season and is not accessible till the mid dry season. Each site consisted of three transects spaced 300 to 500 m apart, each containing 22 Sherman traps, 11 pitfall traps, and 8 Tomahawk traps. Procedures for setting these traps

Table 1. Characteristics of Capture sites.

Characteristic	Description
Vegetation types	There are at least nine vegetation types within the Busanga Flood Plain, with grassland being the most predominant, followed by termitaria and miombo woodland (Mwima, 2006). According to Mwima (2006) grassland is characterized by a distinct expanse of grass cover whose layer is comparatively well developed than the herb and subshrub layer that cover less than 5%. Termitaria has the distinct characteristic of being associated with large termite mounds that can rise up to 6 m with widths of up to 10–15 m (Walker, 2015). Mwima (2006) describes termitaria as bearing a tree, shrub, and grass layer, with the latter two being generally sparse. Characteristic tree species include *Acacia nigrescens, Markamia obtusiforlia, Cassia abreviata, Adonsonia digitata, Euphorbia ingens, Kigelia Africana,* and *Diospyros mespiliformis.* Miombo woodland has an open canopy of trees, with a herb, subshrub, and grass layer that is sparse but very diverse (Mwima, 2006). Characteristic tall trees include *Brachystegia spiciformis, B. boehmii, Julbernardia paniculata, Isoberlina angoiensis, Burkea africana, Parinari curatellifolia, Erythrophleum africanum*, and *Sclerocarya birrea.* As compared to termitaria, miombo has higher tree densities.
Management zones	Four management zones have been prescribed and include zones of intensive utilization by tourism, wild (less used) zones, wilderness (no road access), and special zones (NPWS/JICA, 1999; ZAWA, 2011).
Fire regime	The area is subject to different fire management regimes with different frequencies of burning (Kelly, 2014). "Low fire recurrence" refers to areas where fires occurred in seven or fewer years during the time period from 2000 to 2013. "High fire recurrence" refers to areas with 8 to 14 fires between the year 2000 and 2013. The different types of fire recurrence represent long-term effects of fire. Fire recurrence data was obtained from Kelly (2014) for the period 2000 to 2013 (Figure 1). This period was considered, as this is where most reliable data on fire extents in KNP existed prior to the study.
Fire age	In order to assess short-term effects of fire, trapping sites were further classified based on the time elapsed since the last fire (termed "fire age"). Four categories of fire age were assigned to sampling sites: (1) very recent burn occurring in the midfire season of the same year of trapping; (2) area burnt during the early fire season in same year of trapping; (3) area with fire scars from the previous years' burning season; (4) area without or with very few fire scars from several years ago. The fire history of the sites was based on our own field observations during data collection, verified by park staff and tour operators in the area.

followed protocols described by Stanley, Goodman, and Hutterer (2011) and Stanley and Goodman (2011a, 2011b), who demonstrated the effectiveness of trap and pitfall lines to trap insectivores and medium sized rodents. For rodents, 22 Sherman Live Traps (Large Folding Aluminum Treadles and Doors Galvanized traps [LFA-TDG] $7.5 \times 9 \times 23$ cm) were placed every 5 m on the ground along a 110 m transect. Eight collapsible Tomahawk traps (four traps of $41 \times 13 \times 13$ cm and four traps of $48 \times 15 \times 15$ cm size with one door) were set 5 to 10 m perpendicular to the Sherman trap line. For shrews and rodents that are too small to release the Sherman traps, 50 m pitfall lines were established (Stanley et al., 2011). Each pitfall line consisted of 11 buckets, set 5 m apart, and buried in the ground with the top of the bucket flush with the ground. The 15-l buckets measured 26 cm high, 26 cm in upper diameter, and 24 cm in lower diameter. Traps were exposed for 3 days and nights and were checked twice per day (morning 06–07 hr and evening 16–17 hr), resulting in 99 trap nights for pitfall traps and 270 trap nights for Sherman and Tomahawk traps per site (3 transects × 30 Sherman and Tomahawk traps × 3 nights). Sherman and Tomahawk traps were baited with oats and peanut butter. Pesola precision spring scales (accurate to 0.1 g) were used to measure body mass.

Some animals were sacrificed and specimen was deposited in the collection of Copperbelt University, Zambia. Individuals who were released were marked by fur cuttings to avoid recounting them in case of recaptures. Recaptures were not considered in any of the analyses. Body mass was considered as a proxy for body size. Both measures show allometric relationships to various aspects of animals' ecology and physiology (Brown, 1984; Iskjaer, Slade, Childs, Glass, & Korch, 1989).

Analyses

All data were collated in Microsoft Excel and later uploaded into SPSS 22.0 for statistical analysis. The data from the three transects per site were pooled for statistical analyses. The dependent variables "species richness" and "log body mass" were tested for deviations from normality using Kolmogorov–Smirnov one sample tests. Neither variable deviated from normality ($p = .2$ for both variables).

Composition and Similarities of Small Mammal Communities

Small mammal communities per site were characterized by taxonomic community composition, species richness,

body mass, and functional groups. Taxonomic community composition was described with nonmetric dimensional scaling (NMDS). NMDS integrates community measures, that is, dissimilarity, diversity, and abundance to generate matrices. Differences in species composition between vegetation types and fire effects were determined by permutational multivariate analyses of variance (perMANOVA) used in the function *adonis( )* in R package *vegan* (Oksanen et al., 2015). The analyses were based on community dissimilarity matrices by calculating Bray–Curtis dissimilarities of relative abundance data (Nopper, Ranaivojaona, Riemann, Rödel, & Ganzhorn, 2017). Sites that did not have any species captured were excluded from the analysis. Stress of matrices attained was 0.08. PerMANOVA was used to test for significant dissimilarities between communities in relation to vegetation types, management zones, and fire.

Species Richness

Species richness was used to describe community composition. General linear models were employed to determine whether vegetation types, management zones, and fire recurrence as fixed factors and fire age as continuous variable had an impact on species richness and on the mean body mass of the small mammal community per site. Due to small sample size, it was not possible to include all factors in a single model. We combined vegetation type, fire recurrence, and management zone in various combinations to determine their combined influence on species richness (i.e., vegetation type × fire recurrence; vegetation type × management zone; fire recurrence × management zone). To account for effects of vegetation types without having to enter "vegetation type" as an additional factor, we z transformed species number per vegetation type. This transformed species numbers per vegetation type to z values with a mean of zero and unit variance.

Body Mass and Functional Traits

Body mass and diet were considered as proxies for life history and functional traits. We assessed the influence of vegetation types and fire (recurrence and age) on body mass by calculating the average body mass for each species using only adult animals collected at all sampling sites. Given the small number of individuals caught at most sites, we did not attempt to use body mass as a proxy for body condition or reproductive success that could be used if we had considered juveniles or some kind of measure for body condition. Rather, the average body mass for each species was applied uniformly to the species caught at each of the sampling sites. The mean body mass of the small mammal community per site (=mean of the species body mass of on all species

caught at a site) was calculated as the unweighted mean of the body mass of the species caught per site. Mean body mass per site could not be calculated for two sites of miombo, as no animals had been caught there. Logarithmic transformation to the base of 10 was carried out on mean body mass prior to statistical analyses to achieve normality. To account for effects of vegetation types without having to enter "vegetation type" as an additional factor, we z transformed the mean body mass per vegetation type. This transformed the body mass of species averaged over the species occurring there to z values with a mean of zero and unit variance. Statistical analyses were performed as for species richness. Pearson's correlations were used to assess relationships of fire age to species richness and body mass in the two fire recurrence areas. Kruskal–Wallis analysis of variance was used to determine differences in the representation of dietary guilds between vegetation types.

Functional traits have been compiled from the literature for all small mammal species (Rodentia, Soricomorpha, and Macroscelidea) known from KNP. Species information was obtained from Ansell (1960, 1978); Benadie and Roche (2010); Burda, Zima, Scharff, Macholan, and Kawalika (1999); Chidumayo (1979, 1980); Happold (2013); Happold and Happold (2013); Kawalika (2004); Kingdon (1997); Kingdonet al. (2013a, b); Lancester (1951); Larson (1957); NPWS/JICA (1999); and ZAWA (2013). The information for all species recorded from the region so far has been summarized by Namukonde, Muleya, and Ganzhorn (in press). Given the large number of possible combinations of life history traits, the number of species captured in the present study was too low to analyze associations of most of these traits quantitatively in the context of this study. With the exception of dietary categories, we therefore describe only some traits qualitatively as they seem important to interpret the results of the study.

Results

Composition and Similarity of Small Mammal Communities

During the dry seasons of 2014 and 2015, we captured 105 small mammals belonging to 16 species (11 rodent and 5 shrew species) in the 51 transects assigned to 17 different sites. Even though the inventories were likely to be incomplete, the standardized trapping efforts at all sites should allow robust comparisons between sites and conditions (Tables 2 and 3). The number of individuals caught per site did not differ between vegetation types (Kruskal–Wallis test: $\chi^2 = 3.31$; $p = .19$; $df = 2$), and the number of individuals caught was not correlated with species richness at the sites (Spearman correlation:

Table 2. Trapping Sites with Three Trap Lines Per Site Installed in the Busanga Flood Plain.

Trapping sites	Vegetation type	Fire regime	Fire age	Trapping dates	No. of species/no. of individuals	No. of shrew species/no. of individuals	No. of rodents species/no. of individuals	Coordinates
Iz0H1	Termitaria	Low	4	August 15–18, 2014	3/10	1/4	2/6	S14° 22' 57" E26° 02' 26"
Iz7H1	Termitaria	High	2	August 22–25, 2014	2/3	0	2/3	S14° 23' 39" E26° 03' 16"
W7I3	Termitaria	High	2	October, 18–21, 2015	4/5	1/1	3/4	S14° 12' 31" E25° 39' 22"
Wz0H1	Termitaria	Low	3	October, 22–25, 2014	4/6	0	4/6	S14° 20' 47" E25° 59' 23"
Wz7H1	Termitaria	High	1	August 26–29, 2014	5/9	1/1	4/8	S14° 20' 44" E25° 58' 37"
Iz0C13	Grassland	Low	2	September 18–20, 2015	2/9	0	2/9	S14° 24' 21" E26° 04' 46"
Iz7C14	Grassland	High	2	September, 27–30, 2015	3/21	0	3/21	S14° 23' 28" E26° 03' 49"
W0C10	Grassland	Low	4	August 10–13, 2015	4/9	3/5	1/4	S14° 12' 54" E25° 48' 56"
W7C10	Grassland	High	3	August 6–9, 2015	1/2	0	1/2	S14° 14' 09" E25° 48' 44"
Wz0C13	Grassland	Low	3	September 14–17, 2015	3/8	1/3	2/5	S14° 17' 50" E25° 55' 12"
Wz7C10	Grassland	High	2	August 3–6, 2015	2/3	1/1	1/2	S14° 16' 48" E25° 55' 05"
Iz0D7	Miombo	Low	2	September 24–27, 2015	2/2	0	2/2	S14° 22' 35" E26° 03' 41"
Iz7D7	Miombo	High	3	September 20–23, 2015	1/3	0	1/3	S14° 21' 43" E26° 02' 29"
W0D1	Miombo	Low	2	October 21–24, 2015	1/3	0	1/3	S14° 12' 28" E25° 38' 31"
W7D1	Miombo	High	2	October 15–18, 2015	0	0	0	S14° 13' 23" E25° 36' 53"
Wz0D5	Miombo	Low	1	October 12–15, 2015	2/12	0	2/12	S14° 14' 40" E25° 45' 45"
W70D1	Miombo	High	2	October 25–29, 2015	0	0	0	S14° 15' 19" E25° 47' 39"

Note. Trapping sites are listed using the code names used in the field; Iz = intensive utilization zone, W = wild zone, Wz = wilderness zone; Per site = number of pitfall traps/trap nights = 33/99 and number of traps/trap nights = 90/270 in all sampling sites.

$r_s = .42$; $p = .12$; $n = 15$; the correlation was calculated without the two sites were no animals had been caught).

Of the 105 individuals captured (recaptures were not considered here), we caught 52 (49.52%) in grassland, 33 (31.42%) in termitaria, and 20 (19.05%) in miombo. The species caught in these vegetation types represent a subsample of species known from the region (Namukonde et al., in press). The most abundant species, *Mastomys natalensis*, was captured in all habitats with varying abundances. Its abundance was lowest in miombo, where only one (corresponding to 2.9% of all individuals caught in this vegetation type) individual was trapped. Grassland had the highest abundance of *M. natalensis* (21 individuals, 61.8% of captures), followed by termitaria (12 individuals, 35.3% of captures). The species is known as a generalist that can cope with all kinds of disturbances but seems to be less prone to enter extended forested habitats, as it was caught at all grassland and termitaria sites but was found at only one transect with only one individual in miombo (Table 3). *Mus minutoides* is the smallest rodent and *Crocidura fuscomurina* is the smallest of the shrews caught in the present study (both about 3–4 g). Both species were caught mostly on termitaria and in one grassland transect. Species captured in only one vegetation type included *Crocidura cyaena, C. mariquensis* and *Otomys angoniensis* in grassland and *Steatomys pratensis, Mus triton, Lemniscoyms rosalia,* and *Saccostomus campestris* in termitaria. All species, except for *C.*

mariquensis (that is associated with marshes) can be considered generalists that are expected in a wide range of habitats.

The small mammal communities differed significantly between vegetation types (perMANOVA: $F = 3.34$; $p < .01$; Figure 2). Communities in grassland and termitaria were rather similar while communities of miombo were set apart. This is due to the low number of species caught in miombo, the lack of insectivores caught in this vegetation type and the frequent occurrence of arboreal squirrels (*Paraxerus cepapi*; though squirrels were also caught on one termitaria site). Communities did not differ significantly with respect to management zone, fire recurrence or fire age ($F < 1.18$; $p > .24$ for all three analyses).

Species Richness

The most species rich vegetation type was on termitaria (nine rodent species, two shrew species; mean and standard deviation: 3.6 ± 1.1 species/site; $n = 5$), followed by grassland (five rodents, five shrews; 2.5 ± 1.0 species/site; $n = 6$) and miombo (three rodents, no shrews 1.0 ± 0.9 species/site; $n = 6$; Figure 3). Species richness differed significantly between vegetation types (analysis of variance: $F(2, 14) = 8.97$; $p = .003$).

All subsequent statistical analyses were based on species richness after z transformation per vegetation type to

Table 3. Transect Characteristics and Small Mammal Captures in the Busanga Flood Plains in 2014 and 2015.

Trapping sites	Vegetation type	Fire recurrence	Fire age	Management zone	Mus minutoides	Mastomys natalensis	Saccostomus campestris	Paraxerus cepapi	Lemniscomys rosalia	Mus triton	Aethomys nyikae	Steatomys pratensis	Gerbilliscus leucogaster	Aethomys chrysophilus	Otomys angoniensis	Crocidura fuscomurina	Suncus lixus	Crocidura cyanea	Crocidura mariquensis	Crocidura hirta	Species number	Ominvore	Herbivore	Granivore	Insectivore/carnivore
Iz0HI	T	L	4	Iz	3	3										4					3	2			1
Iz7HI	T	H	2	Iz		2	1														2	1		1	
W7I3	T	L	3	Wz		3				1		1					1				4	2		1	1
Wz0HI	T	H	1	Wz	2	2		3	1							1					5	3	1		1
Wz7HI	T	H	2	W		2	1				1			1						1	4	2		1	1
Iz0CI3	G	L	2	Iz		8					1										2	2			
Iz7CI4	G	H	2	Iz		1					1		19		1						3	2	1		
W0CI0	G	L	4	W		4												2	1	2	4	1			3
W7CI0	G	H	3	W		2															1	1			
Wz0CI3	G	L	3	Wz	1	4										3					3	2			1
Wz7CI0	G	H	2	Wz		2											1				2	1			1
Iz0D7	Mi	L	2	Iz				1					1								2	2			
Iz7D7	Mi	H	3	Iz									3								1	1			
W0DI	Mi	L	2	W									3								1	1			
W7DI	Mi	H	2	W																	0				
Wz0D5	Mi	L	1	Wz		1		11													2	2			
Wz7DI	Mi	H	2	Wz																	0				
Total					6	34	2	15	1	1	2	1	26	3	1	8	2	2	1	3					
Body mass (g)					3.57	24.20	59.00	189.30	43.00	23.00	97.50	20.00	101.64	30.00	112.00	3.06	10.75	8.00	12.00	15.00					
SD					0.59	5.26	7.07	22.13			48.50		36.50	1.41		0.84	0.35	1.41		2.65					
Trophic guild					O	O	G	O	H	O	O[a]	G	O	O	H	I/C	I	I/C	I	I/C					

Note. Captures reflect numbers of individuals; recaptures are not considered. Habitat: T = termitaria, G = grassland, Mi = miombo woodland; Fire recurrence: L = low, H = high; Fire age: (1) very recent burn occurring in the middry season of the same year of trapping; (2) area burnt during the early fire season in same year of trapping; (3) area with fire scars from the previous year; (4) area without or with very few fire scars from several years ago; Management zone: Iz = intensive utilization by tourism, W = wild zone (rarely used), Wz = wilderness (no access). Abbreviations for trophic guilds: O = omnivore, G = ganivore, H = herbivore, I = insectivore, I/C = insectivore/carnivore. Trapping sites are listed using the code names used in the field.

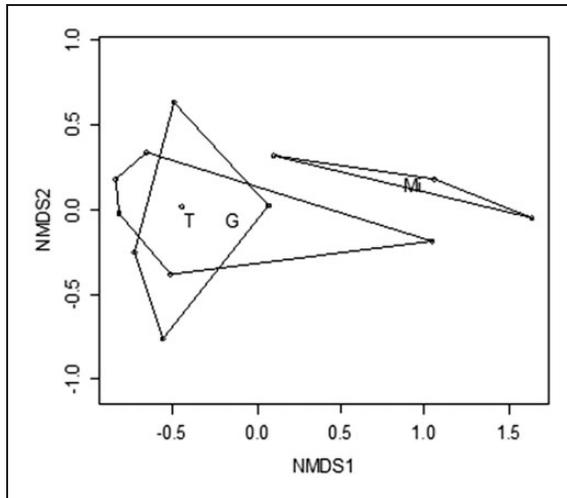[a] Data deficient but classified based on taxonomic affiliation.

Figure 2. Nonmetric dimensional scaling of the small mammal communities in different vegetation types of the Busanga Flood Plain.
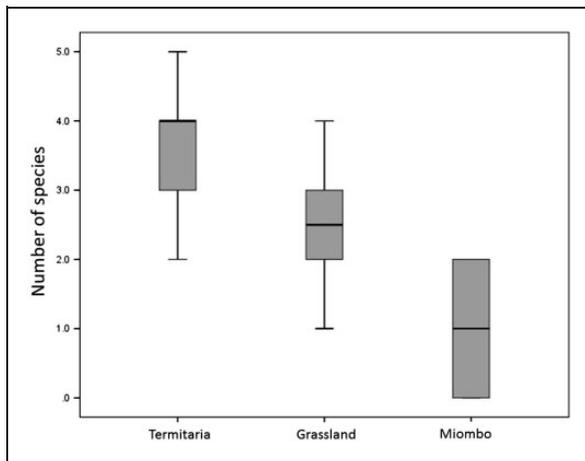

Figure 3. Small mammal species richness in different vegetation types. Values are medians, quartiles, and ranges; $N = 5$, 6, and 6 sites for termitaria, grassland, and miombo, respectively.

Figure 4. Relationship between fire age and small mammal species richness at sites subject to low or high fire recurrence. Species numbers were z transformed per vegetation type. Categories of "fire age": 1 = very recent burn from the mid fire season of the same year of trapping; 2 = area burnt during the early fire season in same year of trapping; 3 = area with fire scars from the previous years' burning season; 4 = area without or very few fire scars from several years ago. ○ = grassland, □ = termitaria, and △ = miombo; open symbols: low fire recurrence; filled symbols: high fire recurrence.

Body Mass and Functional Traits

Based on literature classification of life history traits, small mammals of KNP are predominately omnivorous and nocturnal with body mass ranging from 3.06 g (*Crocidura fuscomurina*) to 189.30 g (*Paraxerus cepapi*; Table 3). The percentage of omnivorous and granivorous species differed significantly between vegetation types (Kruskal–Wallis test: Omnivores: $H = 7.56$; $p = .02$; Granivores: $H = 6.90$; $p = .03$; Figure 5). Granivores were only captured in termitaria and were represented by two species (*Steatomys pratensis* and *Saccostomus campestris*) that shelter in burrows excavated by themselves or by spring hares or aardvarks, in sandy soils or termite mounds (Kingdon et al., 2013a). In the absence of sandy soils as is the case in the Busanga Flood Plain (Mwima, 2016), these two species will most likely burrow in termite mounds.

In grassland, 100% of the species caught were terrestrial and small. In termitaria, most of the small species from the grassland were present plus a few other small terrestrial species. In addition, the large arboreal squirrel *Paraxerus cepapi* has been caught at one termitaria site. None of the small shrews, and only one of the smaller rodent species have been captured in miombo (Figure 6).

The squirrel *Paraxerus cepapi* is the only species classified as truly arboreal. Since, on average, more species were caught at termitaria sites than at miombo sites and

account for differences between vegetation types. Species richness did not differ between management zones, $F(2, 14) = 0.34$; $p = .72$. In single factor analysis, there was a tendency but no significant difference of small mammal species richness between the low and high fire recurrence areas, $F(1, 15) = 7.77$; $p = .07$. As a single factor, fire age was also uncorrelated with species richness (Pearson correlation: $r = -.08$; $p = .75$; $n = 17$). When combining fire recurrence and fire age, the effect of fire recurrence became significant, while fire age remained nonsignificant (General Linear Model [GLM]: fire age: $F = 1.02$; $p = .33$; fire recurrence: $F = 4.66$, $p = .049$; and model: $F = 2.40$, $p = .13$; Figure 4).
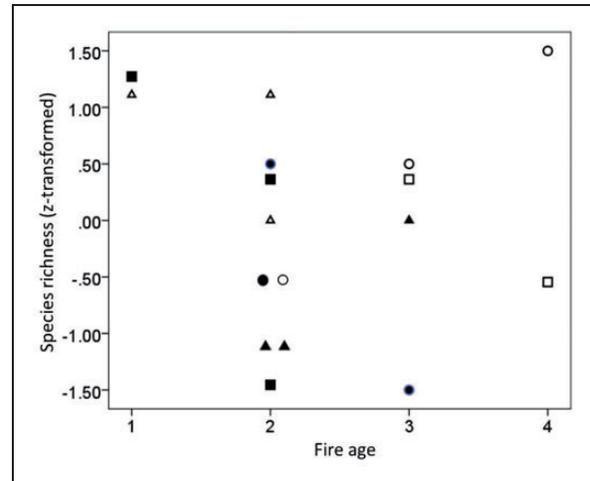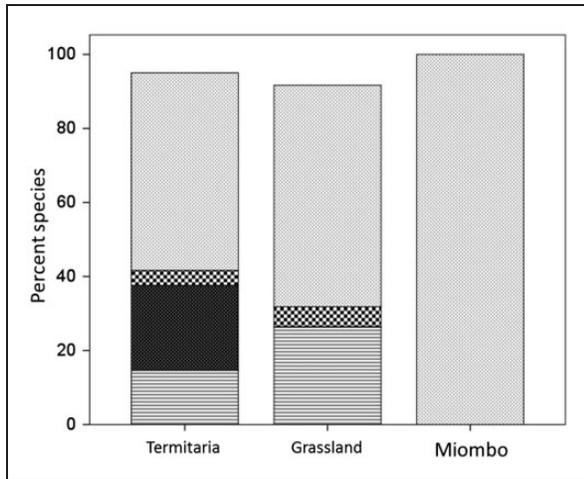
Figure 5. Relative representation of different trophic guilds in different vegetation types. Finely dotted = omnivores, checkerboard = herbivores, black = granivores, and striped = insectivores.
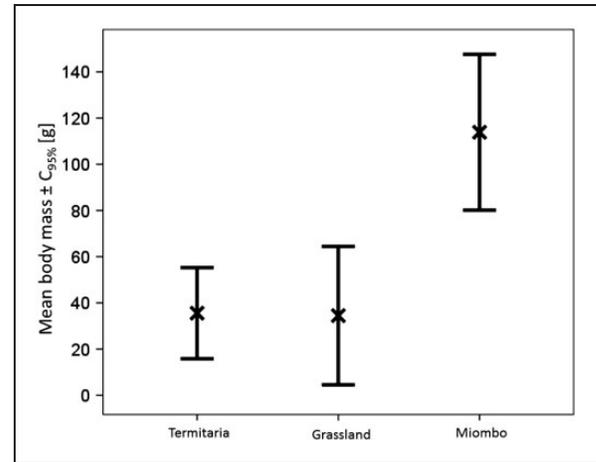

Figure 7. Mean body mass of species in different vegetation types of the Busanga Flood Plain. Values are means and 95% confidence intervals. $N = 5$, 6, and 4 for termitaria, grassland, and miombo, respectively.
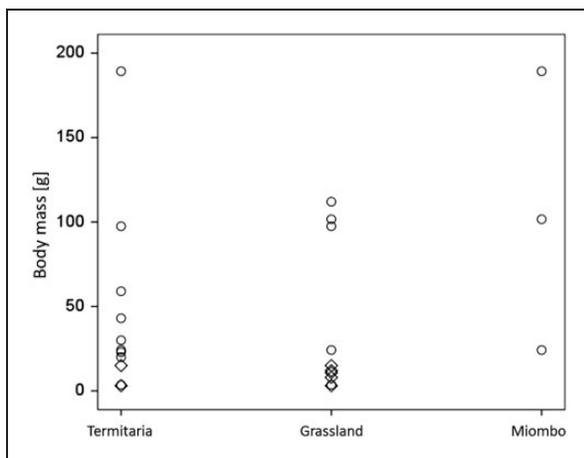

Figure 6. Body mass of species caught in different vegetation types of the Busanga Flood Plain. Each entry marks one species. All individuals of a given species were assigned the same body mass in all vegetation types; ○ = rodents and ◇ = shrews.

since *P. cepapi* was caught only at one termitaria site but at two miombo sites, the relative contribution of this one arboreal species for the termitaria community was lower than for miombo communities, where *P. cepapi* was one of the three species (= 33% of the species) caught in miombo. Due to this unequal representation and since *P. cepapi* has a substantially higher body mass than any of the terrestrial species, average body mass of the small mammal species per site was significantly higher in miombo than at the other sites, $F(2, 12) = 6.74$; $p = .01$; Figure 7.

The allometric relationship between body mass and arboreality would bias any analysis of body mass in

relation to environmental variables. Therefore, all subsequent statistical analyses were based on mean body mass after z transformation per vegetation type to account for differences between vegetation types. Z transformed mean body mass did not differ between management zones, $F(2, 12) = 0.98$; $p = .40$ and fire recurrence, $F(1, 13) = .49$; $p = 51$. Two-way analysis of variance indicated no significant interactions of these factors on body mass (fire recurrence × management zone: $p > .05$). Overall, the mean body mass of small mammal species caught per site decreased significantly with the time elapsed since the last fire (Pearson correlation: $r = -.57$; $p = .03$; $n = 15$). When combining fire recurrence and fire age, the effect of fire age remained significant (GLM: fire age: $F = 5.17$, $p = .04$; fire recurrence: $F = 0.02$, $p = .88$; model: $F = 2.91$, $p = .09$; Figure 8).

Discussion

Fire is an important component of African savannah ecosystems and often used as a management tool for conservation and tourist activities. Yet, the interplay between vegetation and fire and their effects on the diversity and structure of small mammal communities is not understood and studies yielded differing results (e.g., Blaum et al., 2006; Bösing et al., 2014; Decher & Bahian, 1999; Hauptfleisch & Avenant 2015; Joubert & Ryan, 1999; Yarnell, Metcalfe, Dunstone, Burnside, & Scott, 2008). In view of their possible importance for ecosystem processes, we assessed the composition and traits of small mammal communities in the three major vegetation types of the Busanga Flood Plain and assessed the influence of fire (recurrence and age) on their community characteristics. In the Busanga Flood Plain, termitaria
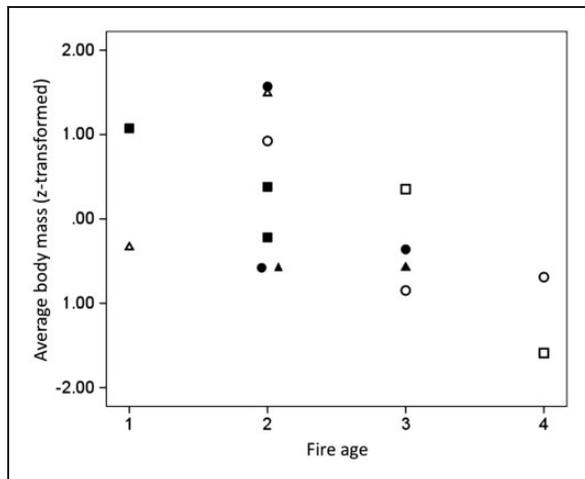
Figure 8. Relationship between fire and averaged body mass of small mammal species per site at sites subject to low or high fire recurrence. Average body mass of small mammal species was *z* transformed per vegetation type. Categories of "fire age": 1 = very recent burn from the mid fire season of the same year of trapping; 2 = area burnt during the early fire season in same year of trapping; 3 = area with fire scars from the previous years' burning season; 4 = area without or very few fire scars from several years ago. ○ = grassland, □ = termitaria, and △ = miombo; open symbols: low fire recurrence; filled symbols: high fire recurrence.

mainly occur as interspaced elevated patches in grasslands that provide islands of refuge in times of floods during the wet season. During the dry season, they might also provide more shelter against fire, as it is easy to dig burrows in the previous termite mounds while the surrounding floodplain can be extremely hard to dig in once the soil has dried out. Thus, termitaria are likely to serve as refuge and source for recolonization of areas after disturbance during the wet as well as during the dry season (Bowland & Perrin, 1993; Parr & Chowan, 2003). This might explain the higher species richness and greater variety of dietary guilds on termitaria than in the neighboring grassland that might need to be recolonized repeatedly during the course of the year.

Miombo occurs at the fringes of the Busanga Flood Plain and as it is structurally enriched with more trees than found in grassland. Due to the increased heterogeneity of the vegetation, we had expected greater species richness of small mammals. Yet this was not the case. While our traps were not designed to catch larger species, the lack of small sized species in miombo is startling. This is even more so as a review of the small mammal inventories in KNP based on published reports had indicated higher species richness for woodlands (Namukonde et al., in press). Miombo is considered a vegetation formation growing on poor soil and thus not being very productive (East, 1984; Desanker, Frost, Justice, & Scholes, 1997; Campbell et al., 2007), while termitaria are characterized

by good soil conditions that promotes plant growth (Otieno et al., 2011). While high productivity soil results in high biomass across trophic levels, the link between productivity and species diversity remains unclear despite decades of research and seems to depend on local conditions, including habitat structure that is likely to obscure productivity—diversity relationships when considered across different vegetation types (Liang et al., 2016, Simons et al., 2017; Socher et al., 2012, 2013; Srivastava & Lawton 1998). Thus, miombo might be as rich in small mammal species as the other two vegetation types, although the densities of the terrestrial small mammals might be lower. If so, our results (low species richness in miombo) might not so much be a consequence of low species numbers occurring in miombo but might be due to low densities of species and therefore low capture rates.

Effects of fire were quite variable. While we were able to estimate fire frequencies, fire intensity could not be measured, though it is likely to be important. Early dry season fires (such as prescribed by the management plan) are less intense and severe than late dry season fires owing to the seasonal differences in the fuel moisture levels and loads (Govender, Trollope, & van Wilgen, 2006; Smit, Asner, Govender, Vaughn, & van Wilgen, 2016). It is assumed that fire intensity has pronounced effects on the distribution and composition of small mammal communities in different habitats. Despite the important role of fire, and probably due to the difficulties in measuring fire properties (such as intensity), the interactions between fire, grazing, and precipitation are still not understood well for large herbivore communities, let alone for small mammals (e.g., Archibald, 2008; Archibald, Bond, Stock, & Fairbanks, 2005). Integrating some kind of indicator for fire intensities at ground level and in the canopy (where applicable) might be a valuable addition to future analyses of fire effects.

To make the analyses more complex, fire does not only act directly simply by burning but also indirectly through reduction in vegetation cover, through reduction in food availability, or fire history can impart demographic legacies on vegetation structure and dynamics, such as documented in Kruger National Park (Levick, Baldeck, & Asner, 2015). On the level of species richness, areas that are burnt frequently in contradiction to the prescriptions of fire management plan of the area had fewer species irrespective of the time elapsed since the last fire had occurred. This might indicate restrictions by fire regimes imposed upon small mammals and might reflect a similar phenomenon as described by Rowe-Rowe (1995) who suggested that species of small mammals are adapted to either frequent or infrequent burning. Despite the extensive trapping effort, we could not identify any species, traits, or combination of traits that would allow describing a pattern in the phenomenon of declining species numbers with increasing fire frequency. The phenomenon

was observed, but our data are too scant to allow for interpretations of this phenomenon based on species identities or species traits.

The representation of species with different body mass found in communities at different times since the last fire has gone through the area might be easier to interpret. As time goes by after a fire, more smaller species were represented in the community (Figure 8). Thus, smaller species seem to be more affected by burning than larger species. A possible explanation could be that smaller species have more problems than larger species to escape fire, and once they are gone, there are very few left to recolonize burnt areas. Also, given that body mass correlates positively with mobility and home range size (Lindstedt, Miller, & Buskirk, 1986; Lomolino & Perault, 2006; Swihart, Slade, & Bergstrom, 1988), larger species have larger home ranges and are more likely to utilize the escape routes provided by the intervening termitaria and to recolonize the area again after fire. Certainly, other traits could also be responsible for the observed differences, such as diet, which determines a species ability to make use of the food resources available after a fire, locomotion, which is linked to the ability to escape disturbance (Golley, Petrusewicz, & Ryszkowski, 1975), or litter size and the number of litters per year, which determines a species ability to counter fire induced mortalities (Plasvic, 2014). Yet, for the Busanga Flood Plain, the information on life history traits of small mammals is too scant to allow further analyses of the interactions between species and environmental characteristics.

Implications for Conservation

Our study demonstrated different responses of different small mammals to the current fire regimes in the Busanga Flood Plain. Specifically, it demonstrates the impact of repeated bushfires on small mammal communities outside the prescriptions of the KNP's Fire Management Plan. It also revealed substantial gaps in our knowledge on fundamental properties of small mammal species, let alone their interactions within this ecosystem. If small mammals react differently to different fire regimes, due to either direct fire effect or indirect effects, such as changes in vegetation characteristics, these different regimes might have long-term consequences that are far from being understood. Further, the vulnerability of small mammal communities to repeated bush fires in the Busanga Flood Plain may increase given the predicted changes in climate to drier and warmer conditions (Government of the Republic of Zambia, 2007; Kalantary, 2010; MacFadyen et al., 2012) that pertain in the late fire seasons and are likely to increase under the current climate scenarios. Given the possible importance of fire and small mammals in ecosystem processes, their interactions will need to be reviewed in more detail.

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