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Assessments, changes, challenges, and solutions

Edited by

Rasmus Revermann¹, Kristin M. Krewenka¹, Ute Schmiedel¹,
Jane M. Olwoch², Jörg Helmschrot^{2,3}, Norbert Jürgens¹

¹ Institute for Plant Science and Microbiology, University of Hamburg

² Southern African Science Service Centre for Climate Change and Adaptive Land Management

³ Department of Soil Science, Faculty of AgriSciences, Stellenbosch University

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The response of small mammal communities to low and high fire recurrences in Kafue National Park, Zambia

Ngawo Namukonde^{1,2*} and Chuma Simukonda³

1 Institute for Zoology, University of Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany

2 School of Natural Resources, Department of Zoology and Aquatic Sciences, The Copperbelt University, P.O. Box 21672, Kitwe, Zambia

3 Department of National Parks and Wildlife, Ministry of Tourism and Art, Private Bag 1, Chilanga, Zambia

* Corresponding author: namukonde@gmail.com

Abstract: To investigate the influence of fire on the communities of small mammals in the Kafue National Park, we trapped 105 individuals (belonging to the families Nesomyids, Murids, Sciurids, and Soricids) in the dry season of 2014 and 2015. We employed 6,273 trap-nights in sites representing three major habitats of small mammals (grassland, miombo woodland, and termitaria) and two fire regimes: namely, high and low fire recurrence. Fire age was assigned based on the last event of fire at a trapping site. These three (vegetation, fire recurrence and age) served as predictor variables, whilst community structure, species richness, and body mass served as response variables. Vegetation had a significant effect on all response variables. Communities in termitaria and grassland overlapped, whilst miombo woodland was set apart. Termitaria was the most species-rich of the habitats and may serve as refugia for species in times of disturbance. In the low and high fire recurrence areas, fire age had different effects on the response variables. In the low fire recurrence areas, species richness increased with time since the last fire occurred, while in the high fire recurrence areas, it decreased accordingly. This could be in response to the reduction in cover available to shelter from predation and other environmental factors, as fire acts to reduce vegetation biomass. This response could also be a function of the animals' life-history traits, particularly of body size, which decreased as time passed since the last fire, implying a higher vulnerability of the smaller-sized species to the current fire regime. Further, fire also had an influence on the dietary resource use of rodents, as they tended to broaden their dietary niches in areas of high fire recurrence compared to low fire recurrence areas. This corroborates the notion that small mammals can cope with either frequent or infrequent burning.

Resumo: Para investigar a influência do fogo nas comunidades de pequenos mamíferos no Parque Nacional de Kafue, capturámos 105 indivíduos (pertencentes às famílias Nesomyids, Murids, Sciurids e Soricids) na época seca de 2014 e de 2015. Aplicámos 6 273 armadilhas em locais que representam três grandes habitats de pequenos mamíferos (prados, bosques de miombo e colónia de térmitas) e dois regimes de fogo, recorrência de fogo alta e recorrência de fogo baixa. A idade do fogo foi atribuída com base no último evento de incêndio num local de armadilhagem. Estas três serviram como variáveis preditivas, enquanto que a estrutura da comunidade, a riqueza específica e a massa corporal serviram como variáveis de resposta. A vegetação teve um efeito significativo em todas as variáveis de resposta. As comunidades em colónias de térmitas e prados sobrepueram-se, enquanto que os bosques de Miombo ficaram à parte. As colónias de térmitas foram as mais ricas em espécies e poderão servir como refúgio para espécies durante períodos de perturbação. Nas áreas de alta e baixa recorrência de incêndios, a idade do fogo teve diferentes efeitos nas variáveis de resposta. Nas áreas de baixa recorrência, a riqueza específica aumentou com o tempo desde o último incêndio, diminuindo nas áreas de alta recorrência. Isto poderá ser o resultado da redução da cobertura disponível para abrigar da predação e outros factores ambientais, pois o fogo reduz a biomassa da vegetação. Esta resposta pode também ser uma função dos seus traços de história de vida, particularmente o tamanho do corpo, o qual diminuiu à medida que o tempo passou desde o último incêndio, implicando uma maior vulnerabilidade das espécies de porte pequeno aos regimes actuais de fogo. Além disso, o fogo teve também uma influência no uso dos recursos dietários pelos roedores, pois estes tenderam a alargar os seus nichos dietários em áreas de alta recorrência de fogos, em comparação com áreas de baixa recorrência. Isto corrobora a noção de que os pequenos mamíferos podem tanto lidar com incêndios frequentes como infrequentes.

Introduction

Small mammals assume various roles in ecosystem functioning. They act upon plant communities due to herbivory and seed predation (Young et al., 2015), as agents of soil aeration and creation through their burrowing activities (Martin, 2003; Kalies & Covington, 2012), pests and pest controllers through their consumption of large amounts of vegetation and invertebrates (Seig, 1987; Timbuka & Kabigumila, 2006), and as food for a variety of predators in ecosystems (Happold, 2013; Happold & Happold, 2013). Yet their importance in ecosystems such as the Kafue National Park (KNP) is often overlooked, as they do not attract as much attention compared to the large charismatic species in the park. Further, they are often considered to be vermin, appearing to benefit from human disturbances in contrast to the large mammals (Young et al., 2015).

Yet as with larger species, many small mammals may also be vulnerable to anthropogenic impacts. Reasons for this vary between sites and small mammal communities (Swihart et al., 1988; Rowe-Rowe, 1995; Bösing et al., 2014; Young et al., 2015; Namukonde et al., 2017). Bush fires represent one such potential anthropogenic disturbance and are a common phenomenon in the KNP, occurring annually (Kelly, 2014). Fire is used by the park's management for a number of purposes, including to: (1) reduce the impact of late dry season fires, (2) improve visibility for photographic tourism, and (3) provide fresh fodder for game (NPWS/JICA, 1999; Kampamba et al., 2005; Chanda, 2007). Since very little is known about the influence of these fires on small mammal species and their community characteristics, we studied the effect of repeated bushfires on their community properties in the Busanga Flood Plain (BFP) of the KNP.

Methods

Trapping sites were selected based on vegetation, land use, and fire regime. Vegetation descriptions followed Mwima (2006); land use was set out as prescribed



Figure 1: Pitfall lines in (a) grassland and (b) miombo woodland.

by the management zones of Kafue National Park (NPWS/JICA, 1999; ZAWA, 2013); and fire recurrence was established using remote sensing data compiled by Kelly (2014). In each of the vegetation types (grassland, termitaria, and miombo woodland), replicate trapping sites were set in areas of low and high fire recurrence. Sites that experienced fewer than eight years of fire between the years 2000 and 2013 were classified as low fire recurrence sites and those that experienced eight or more fires during this period were classified as high fire recurrence sites.

For each site, the age of fire was assigned as 'fire age' from 1 to 4 (1=very recent fire occurring few weeks prior to trapping, 2=site burnt during the early fire season, 3=site burnt in the previous year, and 4=site without fire scars or scars from several years ago). This categorisation was based on the researchers' own

field observations and was verified by park staff and tour operators in the area. At each of these sites, three transect lines were established, each with 11 pitfall traps (11 x 15-liter buckets), 22 Sherman (22x LFA-TDG 7.5 x 9 x 23 cm) and 8 Tomahawk (four TH 41 x 13 x 13 cm and four TH 48 x 15 x 15 cm sized with one door) live traps baited with peanut butter and oats, following methods outlined by Stanley and Goodman (2011 a, b) and Stanley et al. (2011). Pitfall traps targeted shrews and rodents that were too small to trigger trap doors in the Sherman and Tomahawk traps. The latter two trap types were set with the intention of trapping medium-sized rodents. Trapping was conducted in the dry season of 2014 and 2015, as the BFP is inaccessible during the wet season. All traps were set for three days and nights consecutively and were checked twice per day (morning 06–07 hr and evening 16–17 hr). The

number of traps set was small, a deliberate decision to enable a standardised trapping approach that could be applied at all sites and conditions. Although the inventories were likely to be incomplete, the standardised trapping efforts at all sites should represent representative sampling that allows robust comparisons between sites and conditions. Figure 1 provides a depiction of the trap lines set in grassland and miombo woodland.

In order to determine the dietary resource use of the small mammals in areas of high and low fire recurrence, we employed stable isotope biochemistry techniques. This technique provided quantitative records of the feeding ecology of each species based on the stable isotopes of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) found in the rodents' hair tissue. Values of $\delta^{13}\text{C}$ reflected the carbon source of the animal's food, whilst $\delta^{15}\text{N}$ reflected its trophic positioning in a community (Fry, 2008; Crowley, 2012; Namukonde et al., 2018).

Coexisting species avert competition for habitat resources through trophic specialisations (MacArthur & Levins, 1967) and through differences in their body mass and sizes (Hutchinson, 1959), which reflect their niche differences. Niche width reflects the dietary space or length a species inhabits. Here the standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of species that had more than two individuals trapped in low and high fire recurrence area was used to describe the niche widths. Linear models and multivariate analysis were used to assess the effect of vegetation, land use, and fire on the community measures.

Results

During the study period, 105 individuals (recaptures not included) belonging to 16 species (11 rodent and 5 shrew species) of small mammals were captured in 51 transects laid in the 17 trapping sites in

termitaria, grassland, and miombo woodland vegetations (Table 1).

Ubiquitous species trapped included *Mastomys natalensis*, whose abundance varied between the three vegetation types. Except for the bush squirrel (*Paraxerus cepapi*), which is arboreal, all the captured species were terrestrial. The bush squirrel was the largest species ($189 \pm 22\text{g}$) trapped and was found in termitaria and miombo woodland only. The smallest species (3–4 g) captured were *Mus minutoides* (rodent) and *Crocidura fuscomurina* (shrew). These species were trapped mostly in termitaria and in only one transect in grassland. Community structure and composition of the small mammals differed significantly between the three vegetation types (per MANOVA: $F = 3.34$; $p < .01$, Fig. 2). Communities in termitaria and grassland had overlaps whilst miombo woodland was set apart. Termitaria was the most species-rich (3.6 ± 1.1 species/site) habitat, followed by grass-

Table 1: Transect characteristics and small mammal captures in the Busanga Flood Plains in 2014 and 2015. 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 mid dry 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: lz = intensive utilization by tourism, W = wild zone (rarely used), Wz = wilderness (no access) (Source: Namukonde et al. 2017).

Trapping sites	Vegetation type	Fire recurrence	Fire age	Management zone	<i>Mus minutoides</i>	<i>Mastomys natalensis</i>	<i>Saccostomus campestris</i>	<i>Paraxerus cepapi</i>	<i>Lemniscomys rosalia</i>	<i>Mus triton</i>	<i>Aethomys nyikae</i>	<i>Steatomys pratensis</i>	<i>Gerbilliscus leucogaster</i>	<i>Aethomys chrysophilus</i>	<i>Otomys angoniensis</i>	<i>Crocidura fuscomurina</i>	<i>Suncus lixus</i>	<i>Crocidura cyanea</i>	<i>Crocidura mariquensis</i>	<i>Crocidura hirta</i>	Species number	
Iz0H1	T	L	4	lz	3	3										4					3	
Iz7H1	T	H	2	lz		2	1															2
W7I3	T	L	3	Wz		3				1	1	1										4
Wz0H1	T	H	1	Wz	2	2		3	1							1						5
Wz7H1	T	H	2	W		2	1							1							1	4
Iz0C13	G	L	2	lz		8					1											2
Iz7C14	G	H	2	lz		1							19		1							3
W0C10	G	L	4	W		4												2	1	2		4
W7C10	G	H	3	W		2																1
Wz0C13	G	L	3	Wz	1	4										3						3
Wz7C10	G	H	2	Wz		2											1					2
Iz0D7	Mi	L	2	lz				1					1									2
Iz7D7	Mi	H	3	lz									3									1
W0D1	Mi	L	2	W									3									1
W7D1	Mi	H	2	W																		0
Wz0D5	Mi	L	1	Wz		1		11														2
Wz7D1	Mi	H	2	Wz																		0
Total					6	34	2	15	1	1	2	1	26	1	1	8	1	2	1	3		105
Proportion relative to the total captured (%)					5.7	32	1.9	14	1	1	1.9	1	25	1	1	7.6	1	1.9	1	2.9		
Body mass (g)					3.6	24	59	189	43	23	98	20	102	30	112	3.1	11	8	12	15		
SD					0.6	5.3	7.1	22			49		37	1.4		0.8	0.4	1.4		2.7		
Trophic guild					O	O	G	O	H	O	O*	G	O	O	H	I	I	I	I	I	I/C	

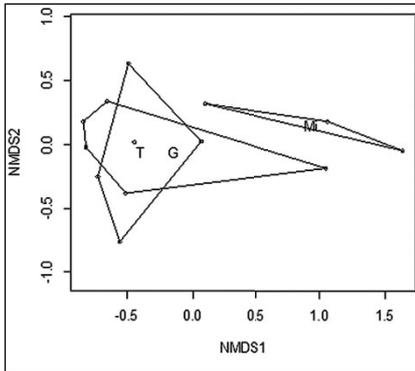


Figure 2: Small mammal communities in different vegetation types (Source: Namukonde et al., 2017).

land (on average 2.5 ± 1.0 species/site) and miombo (1.0 ± 0.9 species/site). Species richness differed significantly between the three vegetation types (ANOVA: $F_{2,14} = 8.97$; $p = .003$).

As a single factor, fire recurrence had no significant influence on the species richness ($F_{1,15} = 7.77$; $p = 0.07$) of small mammals; neither was fire age correlated to species richness (Pearson correlation: $r = -0.08$; $p = 0.75$; $n = 17$). However, when the two factors were combined, the effect of fire recurrence became significant (while fire age remained non-significant [GLM: fire age: $F = 1.02$; $p = 0.33$; fire recurrence: $F = 4.66$, $p = 0.049$; model: $F = 2.40$, $p = 0.13$]). In the low fire recurrence areas, species richness was positively correlated to fire age, whereas in the high fire recurrence area, the opposite was observed (Fig. 3).

Because species varied between sites, we replaced species identities with life history traits, such as body mass, social systems, activity patterns, diet, habitat uti-

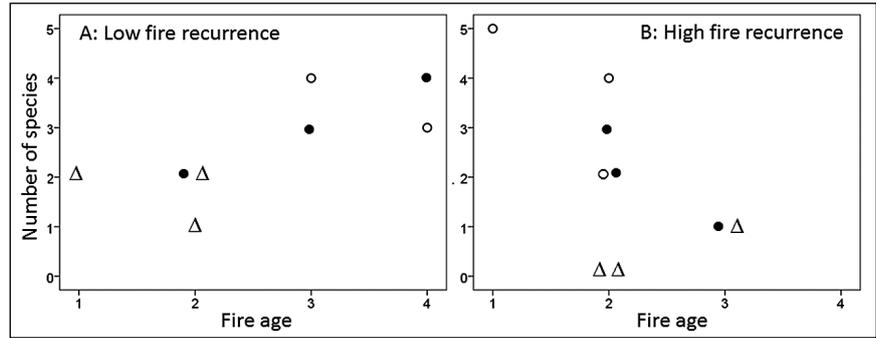


Figure 3: Relationship between fire and small mammal species numbers at sites subject to low fire recurrence (A) and high fire recurrence (B). Categories of "Fire age": 1: very recent burn from the mid fire season of the same year of trapping; 2: area burnt during the early fire season in same year of trapping; 3: area with fire scars from the previous years' burning season; 4: area without or very few fire scars from several years ago; O = termitaria, ● = grassland, Δ = miombo.

lisation, locomotion, and litter size (Violle et al., 2007; Namukonde et al., in press). For body mass, the evidence pointed to smaller-sized species being most affected by the current fire regime. The average body size decreased with increasing time after a site had experienced fire (Fig. 4).

Regarding dietary resource use, rodent species tended to broaden their dietary niches in areas of high fire recurrence

compared to areas of low fire recurrence. This was evident for seven out of eight comparisons ($p = .035$, Sign test, Fig. 5), with the exception being *Mus minutoides*, which had a smaller standard deviation in $\delta^{13}C$ in areas of high than in areas of low fire recurrence. All of these rodents are omnivores. For shrews (*Crocidura fuscomurina*), the pattern was reversed; shrews are predominately insectivores.

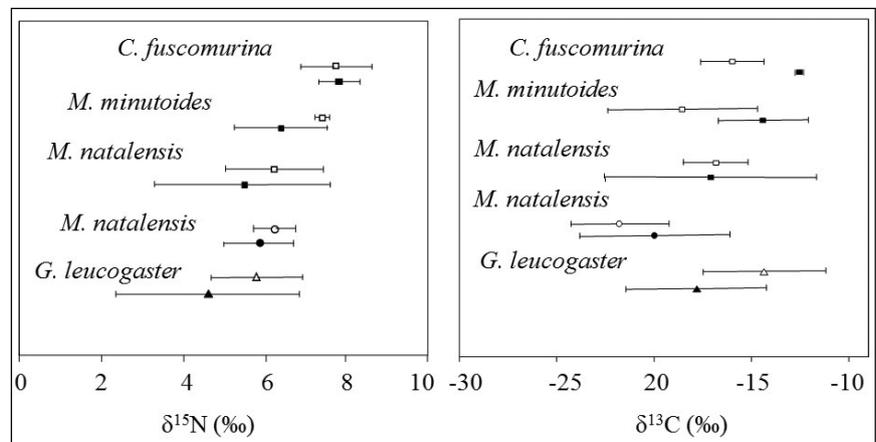


Figure 5: Niche width indicated by $\delta^{15}N$ (A) and $\delta^{13}C$ (B) in high and low fire recurrence areas. O = grassland, □ = termitaria and Δ = miombo; open symbols: low fire recurrence, filled symbols: high fire recurrence. Values are means and standard deviation. (Source: Namukonde et al., 2018).

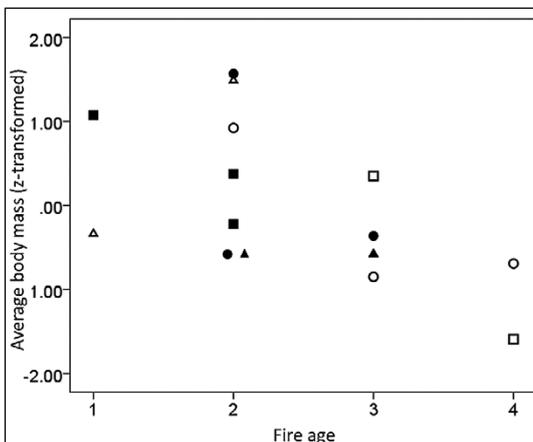


Figure 4: Relationship between fire and mean body mass of small mammal species at sites subjected to low or high fire recurrence. Average body mass of small mammal species was z-transformed per vegetation type. Categories of "Fire age": 1: very recent burn from the mid fire season of the same year of 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. O = grassland, □ = termitaria, Δ = miombo; open symbols: low fire recurrence, filled symbols: high fire recurrence (Source: Namukonde et al., 2017)

Discussion

The high species richness of termitaria was thought to be influenced by their ecological function as refugia against disturbance (e.g., flooding and fire) and as sources of recolonisation (Namukonde et al., 2017). Termite mounds are a prominent feature of termitaria and, owing to their structure, they are likely to offer underground shelter to small mammals. They also tend to have more friable soils that are easier to dig as compared to those in the grasslands of flood plains. Moreover, in the wet season and in times of floods, their elevation offers dry ground.

Though most large mammals seem adapt to fires (Green et al., 2015), small mammals are seemingly affected by its effect on cover, particularly its reduction (Swanepoel, 1981; Yarnell et al., 2007, 2008). Land transformation due to high or low recurrent fire frequencies often leads to different responses between small mammal species (Fig. 3 & 4; Rowe-Rowe, 1995; Young et al., 2015; Namukonde et al., 2017). This supports predictions regarding the shift of community composition and structure of small communities in the park based on the evidence pointing to the significant differences in primary productivity between frequently burnt areas and areas that do not experience frequent fires (D. Kuebler, University of Hamburg, unpubl. data). According to Moss (1973) and Chanda (2007), fires occurring in areas of high fire recurrence have the potential to alter the range land into more open areas. Thus, based on the foregoing and considering the lean resources available to manage fires in the park, perhaps emphasis should be placed on important habitats such as termitaria, whose perceived role as refugia for species from disturbance and recolonisation is reaffirmed by the overarching structure of the dietary space assumed by communities of rodents and shrews over those in miombo woodland and grassland (Namukonde et al., 2018).

Fire also affects the dietary resource use of rodents. In areas of high fire recurrence, rodents had broader dietary niches than in areas of low fire recurrence (Fig. 5). This suggests that competition for resources may be relaxed as species do

not need to occupy specific and exclusive niches, because fire acts as a temporal and spatial disturbance in the context of stochastic community processes (Begon et al., 2006; Namukonde et al., 2018). This is an important finding, as it provides an understanding of the boundary conditions under which small mammals reach their carrying capacity in this ecosystem. However, there may be other ecological processes working to depress the populations of rodents from reaching their carrying capacities in the high fire recurrence areas. As pointed out previously, habitat conditions (i.e., availability of cover to avert predation and food to sustain populations) may also contribute to depressing the rodent populations in high fire recurrence areas. Needless to say, these processes are also present in low fire recurrence areas.

For shrews (*Crocidura fuscomurina*), the opposite condition persists as they appear to have narrower dietary niches in areas under high fire recurrence. According to Namukonde et al. (2018), this shrew's niche width is seemingly unaffected by competition, as it is clearly separated from other shrews by body mass following Hutchinson's rule (Hutchinson, 1959). Hutchinson's rule states that species can coexist if they differ in body mass by a factor of two or more, or in linear body size dimensions by a factor of 1.4. This is an important finding, as it, too, provides an understanding of the boundary conditions under which small mammals reach their carrying capacity in this ecosystem.

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