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Small mammal species diversity and distribution in the Selous ecosystem, Tanzania

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Threats to ecosystems are ever increasing from different drivers mostly being linked to anthropogenic activities. This has brought about various measures to restore/protect the wildlife in these areas. Considering the background of most protected areas in East Africa, small mammals have been given least attention, compared with large mammals, although they play a fundamental role in maintaining ecosystem health. It is therefore necessary to understand how small mammals are distributed in any given ecosystem as a baseline information to enable holistic and informed management. We investigated the diversity and distribution of small mammals in Selous ecosystem, Tanzania. Two methods were used; Capture Mark Recapture (CMR) using grids of 70 m × 70 m and random placement of havahart traps in the selected habitats. Between July 2018 and June 2020, a total of 887 individuals belonging to 20 species were captured in 28 224 trap nights with 3% trap success. The small mammal species captured comprised of rodents (91.8%), Macroscelidea (3.9%), Carnivores (2.4%) Eulipotyphla (1.6%), and Primates (0.3%). *Acomys ngurui* (36%) and *Aethomys chrysophilus* (17%) were the most captured species, whereas *Atilax paludinosus* (0.23%), *Helogale pervula* (0.23%), *Rattus rattus* (0.23%) and *Galerella sanguinea* (0.11%) were the least contributing species. *Acomys ngurui* and *Lemniscomys rosalia* were the most distributed species occurring in all four habitats, whereas *Cricetomys ansorgei*, *Rattus rattus*, *Mungos mungo* and *Genetta genetta* had low occurrence. *Grammomys selousi* is reported for the first time in the northern part of the Rufiji River. *Acomys ngurui* abundance differed significantly (χ^2 = 12, df = 3, *p* = 0.007) between the four habitats being higher in the seasonal riverine forest and across seasons (χ^2 = 6, df = 2, *p* = 0.049), with more individuals occurring in the wet season. The Sable Forest habitat had the highest species diversity (*H′* = 2.065) and the lowest diversity (*H′* = 1.506) was recorded in perennial riverine forest/thickets. The highest species diversity (*H′* = 1.65) was recorded in the dry season and the lowest diversity in the wet season (*H′* = 1.445). Most small mammals were associated with seasonal riverine forest than other habitats. Overall, the results from this study show that, the park is rich in small mammal fauna. Therefore, considerations in updating the General Management Plan (GMP) and other plans to include the small mammals in the park management actions is recommended.

Keywords: abundance, diversity, Mammalia, riverine forests, small fauna

Introduction

Historically the protected areas (PAs) in East Africa were meant for large mammals (Caro 2001). This approach has been inherited and has led to inadequate attention to other components of ecosystems, such as small mammals and herpetofauna (Deventer and Nel 2006; Venance 2009; Heinze et al. 2010). According to Fitzherbert et al. (2006) and Marrocoli, (2011), little has been done on small mammals particularly in the tropics and miombo areas. Small mammals play a fundamental role in ecosystem health through their interactions with the habitat in which they live through maintaining food webs and chains (Makundi et al. 2009; Heinze et al. 2010; Marrocoli 2011; Yihune and Bekele 2012; Bösing et al. 2014). Furthermore, because of their greater diversity in morphology, physiology, behavior and life history strategies (Cramer and Willig 2002), and their feeding behaviour (most of them are omnivorous, consuming vegetation, fruits, seeds, and animal prey), they have managed to thrive successfully in different environmental conditions (Hope and Parmenter 2007; Alemayehu and Bekele 2013). In Africa 395 species of rodents have been described and 111 in Tanzania (Senzota et al. 2012; Happold 2013). Nevertheless, with the advancement in molecular genetics the figures might increase significantly (Verheyen et al. 2007; Hoffmann et al. 2010; Denys et al. 2011).

Small mammal species, in particular rodent abundance and diversity, are influenced by a number of factors, which include vegetation type and density, rainfall patterns, temperature variability and soil types (Massawe et al. 2008; Makundi et al. 2009; Alemayehu and Bekele 2013). For example, in central Tanzania, *Arvicanthis neumanni* breeding has been reported to respond to seasonal changes (Massawe et al. 2007). The reason is the influence of rainfall on food, which increases in terms of quality and quantity; however, this is dependent on species and habitat (Kingdon 1974; Mrosso 2004). Overall, rodents' breeding reaches a peak towards the end of the rain season when resources are abundant but seasonal rainfall can be variable (Alemayehu and Bekele 2013). Besides rainfall, the resources in a given habitat are further determined by other environmental variables, such as slope, aspect, elevation and soils among others. During harsh weather conditions, mountains offer refuge to many small mammals (Mulungu et al. 2008). Also, the current unpredictable climatic events shape the diversity and distribution of small mammals (Witecha 2011).

Selous ecosystem occupies a major part of south-eastern Tanzania. The ecosystem is formed by various categories of protected areas, which include National Parks (Nyerere, Mikumi and Udzungwa), Game Reserve (Selous), Forest Reserves (Mkulazi and Magombera), approximately eleven (11) Wildlife Management Areas (WMAs) and a Game Controlled Area (GCA), which harbors a Ramsar site (Kilombero). The ecosystem possesses diverse flora dominated by miombo woodland (McGinley 2008; UNEP-WCMC 2011). Although various studies on small mammals fauna in the Selous ecosystem have been conducted, including Mikumi National Park in the Selous–Niassa corridor (Venance 2009), southern Tanzania (URT 2010) and in the north-eastern sector near Kingupira (Denys et al. 2011), the south-eastern part of Tanzania is among the least researched areas on small mammal ecology (Denys et al. 2011). Considering its size and diverse habitats, it may be home to an, as yet, undiscovered small mammal species. For example, a new Murid species (*Grammomys selousi*) was described in the Selous ecosystem in a small area around Kingupira (Denys et al. 2011). On the other hand, the current climate change trend is reported to pose a serious threat to small mammals and their habitat (Witecha 2011). Therefore, this study aimed at detailing the diversity and distribution of small mammals in the ecosystem for informed and holistic ecosystem management. Specifically, the study was conducted in the Nyerere National Park (NNP), which is the largest national park in Tanzania. The established park forms part of the Selous Game Reserve, a renowned World Heritage Site since 1982 (UNESCO–WHC 2014). Our study aimed at answering the following key questions:

(i) What species of small mammals are represented in the NNP?
(ii) How are they distributed across the different habitats within the park?
(iii) How does habitat and seasons affect their distribution in the park?

Materials and methods

Study area

The study was conducted between July 2018 and June 2020 in four habitats in the Selous ecosystem, specifically in the Nyerere National Park (NNP) (Figure 1), which covers an area of approximately 32 000 km^2. It is located in the south-eastern part of Tanzania between 7°20′ S to 10°30′ S and 36°00′ E to 38°40′ E (MNRT 2012). The park falls within the bimodal rainfall belt of southern Tanzania and annual rainfall ranges from 750 mm in the east to approximately 1 300 mm in the west, falling mainly between mid-November and mid-May (Jihnson 2003). The park forms part of the former Selous Game Reserve (SGR), which constitutes globally important vegetation types that are between the Somali-Maasai and Zambezian regional centres of endemism, but predominantly incorporating the latter (URT 2005). The area possesses diverse flora with an estimated total of >2 000 species (McGinley 2008). The ecosystem harbours significant populations of wildlife, including species classified as Vulnerable (e.g. African elephant, *Loxodonta africana africana*), Endangered (e.g. African wild dog, *Lycaon pictus*) and Critically Endangered (Black rhinoceros, *Diceros bicornis minor*) (UNEP-WCMC 2011). There are approximately 450 bird species that are rare and endemic to the area, which makes this area one of the few Important Bird Areas (IBA) in the region (Briggs 2008). The miombo woodland is dominated by *Brachystegia spicifomis, Julbernardia globiflora, Afzelia quanzensis, Pterocarpus angolensis* and *Salvadora perisca*. Common grasses are *Hyparrhenia newtonii, Andropogon gyanus* and *Hyparthelia dissoluta* (URT 2005). The dominant soils are black cotton with rough slopes characterised by rock outcrops in most parts.

Study habitats

Matambwe closed woodland (CLW) is located at 7°30′44.1″ S, 37°36′7.2″ E, with an elevation of 324 m amsl is a habitat associated with mountains, which form a large part of the northern part of NNP. Nyamambi and Matambwe are within the Eastern Arc Mountain ranges approximately 50 km south of Uluguru Mountain ranges. The area is characterised by mixed vegetation dominated with *Brachystegia spicifomis, Julbernardia globiflora, Afzelia quanzensis, Pterocarpus angolensis*, and *Salvadora perisca* and the common grasses are *Hyparrhenia newtonii, Andropogon gyanus* and *Hyparthelia dissoluta*. The dominant soils are black cotton with rough slopes characterised by rock outcrops in most parts.

Sable forest (FOR) is located at 7°30′56.3″ S, 37°40′33.1″ E, with an elevation 239 m amsl. The area is within a forest dominated by *Afzelia quanzensis*, *Sclerocarya birrea* and *Markhamia zanzibarica*. Soils are mostly black cotton.

Matambwe seasonal riverine forest (SRF) is located at 7°31′48.6″ S, 37°45′54.6″ E, with an elevation of 176 m amsl is dominated by *Steculia apendiculatas*, *Kigelia africana*, *Markhamia zanzibarica*, *Adansonia digitata* and *Combretum* spp. thicket. The habitat is characterised by high percent of leaf litter in the dry season and soils are dominated by sandy loam in most parts.

Rufiji perennial riverine forest/thickets (PR) is located at 7°46′57.5″ S, 37°55′47.1″ E, with elevation of 79 m amsl and extends approximately 50 km along the Rufiji River in both the Selous Game Reserve and Nyerere National Park. The area is characterised by *Adansonia digitata*, *Combretum* spp. thickets, *Borassus aethiopum* and *Hyphaene* sp. palms are the dominant vegetation. The area is limited in undergrowth in most parts with rock outcrops and rough terrain caused by sporadic runoffs in some areas.

Small mammals trapping

Although a number of definitions of small mammals have been proposed by considering weight; 5 kg and less and 500 g or less (Lidicker 2011; Lim and Pacheco 2016), in

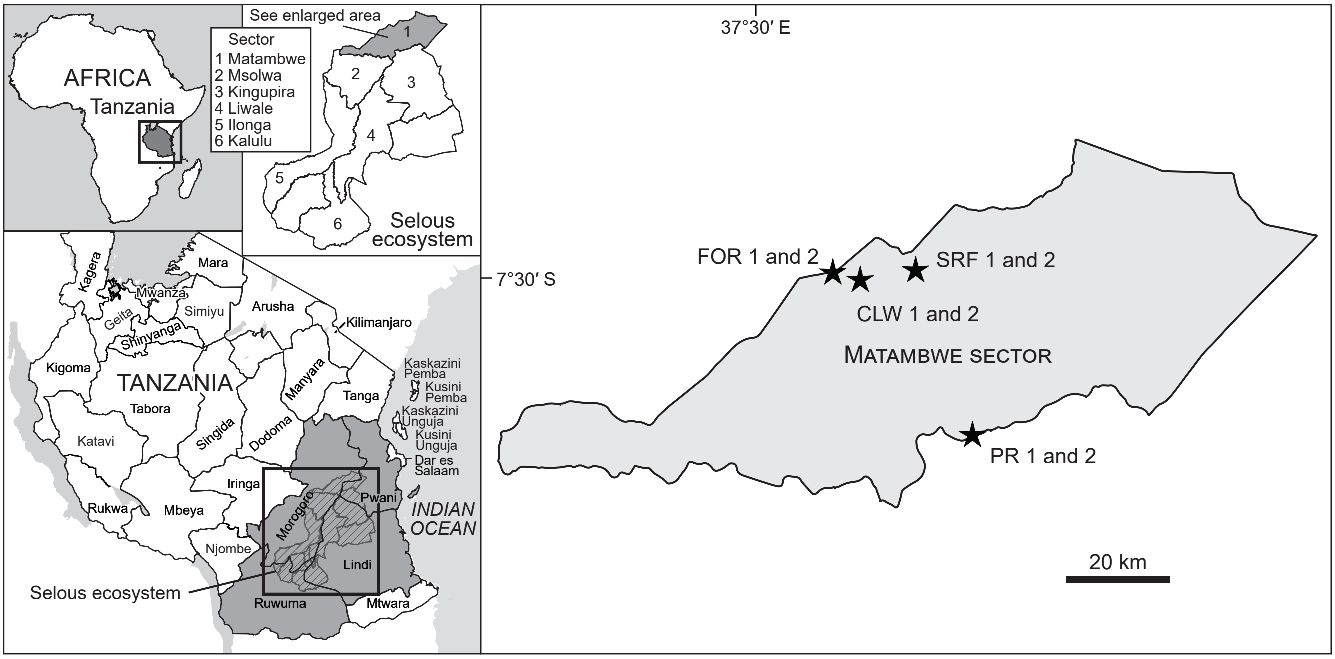

Figure 1: Sampling site locations in the Matambwe Sector in the Nyerere National Park in the Selous ecosystem, Tanzania (SRF = seasonal riverine forest, CLW = closed woodland, PR = perennial riverine forest/thicket and FOR = Sable forest)

this study, small mammals were defined as all mammal species that could be trapped using medium sized (LFA, 7.5 × 9 × 23 cm) Sherman traps (HB Sherman Inc.) and Havahart traps (60 × 15 × 170 cm). Capture-Mark-Recapture (CMR) was also used in this study. In each habitat, two grids of 70 m × 70 m were established with seven parallel lines at a distance of 10 meters apart. Each line had seven trapping stations and in total 49 stations was established in each grid following Hoffmann et al. (2010). Each trapping station was marked by coordinates using Global Positioning System (GPS) to help locate the traps because most of them were set under herbs/cover to protect them from direct sunlight and predators. Every trap was baited using a mixture of peanut butter and maize bran. All traps were checked before 10h00. Trapping was conducted at four–week intervals for three consecutive nights in each trapping session from July 2018 to June 2020. Slices of carrot/sweet potatoes and banana were used as bait in Havahart traps. Identification of captured species in the field followed available distribution maps as provided by Kingdon (1997, 2015) and experts from the Pest Management Center at Sokoine University of Agriculture. Sex, reproductive condition and weight (to the nearest gram) were recorded. The animals were marked by toe clipping and released at the site of capture. Toe clipping was used because it provides an additional advantage for genotyping and it has been proved to cause minimal impact to animals (Borremans et al. 2015). The clipped toes were preserved in 70% alcohol and shipped to the Czech Republic for species confirmation using molecular (Cytochrome b) techniques. The remaining samples are stored at Sokoine University of Agriculture, Pest Management Center Morogoro, Tanzania for later analysis.

Habitat characterisation

Various characteristics of each habitat were collected at five meters radius (modified from Decher and Bahian (1999)) from each trapping station. The recorded variables were number of termite mounds, trees (the dominant species in the specific habitat) and dead logs, visual estimation of percentage canopy cover, shrubs and herbs cover and grass cover and rock outcrops and bare ground percentage. The collected information was used to assess the relative association between species and habitat.

Data analysis

Species composition and trap success

Small mammal species composition was estimated as the total number of different species and their percentage contribution in that community in different habitats. Trap success (TS) was expressed as the proportion of captured animals relative to the number of nights following Telford (1989) expressed as:

$$TS = NS/TN \times 100$$

where, NS is number of individuals captured in a given time and TN is the number of trap nights.

Acomys ngurui abundance

Species abundance was estimated using Minimum Number Alive (MNA) for the most captured species and occurring in all four habitats using CMR history data. We used the Friedman chi-square test to detect *Acomys ngurui* abundance variation among habitat types and season categories. We used robust linear regression model by using the rlm() function in R (R Core Team 2020) to assess the monthly abundance trend of *A. ngurui*.

Species richness, diversity and evenness

Species richness was estimated as number of different species captured in the study area. To assess sampling effort of small mammals, species accumulation curves were constructed using PAST. Species richness was determined using Jackknife and Bootstrap estimators in PAST. Diversity was computed using the Shannon–Wiener index (H') expressed as:

$$H' = -\Sigma(p_i)(\ln p_i)$$

where, $i = 1$, p_i is the proportion of individuals of the ith species or the abundance of the ith species expressed as the proportion of the total individuals, and ln is the natural log of individual proportion. Species evenness (E) was estimated as follows:

$$E = H'/H_{\max}$$

where,

$$H_{\max} = \ln(s)$$

and s = species richness.

Small mammal community similarity and species habitat association

Species community similarity was determined using the Bray–Curtis similarity index (0–1) where 0 indicates identical communities and 1 indicates different communities. A hierarchical clustering analysis was used to show the community similarity. We used a principle component analysis to assess the species–habitat variables association. An ordination technique; Non-Metric Multidimensional Scaling (NMDS) was used to present the associations among habitat covariates and species in different habitats using the vegan package in R version 3.4 (R Core Team 2020).

Statistical analyses

The Shapiro test function in R software (R Core Team 2020) to test for normality of *A. ngurui* abundance. We used the Kruskal–Wallis test to compare the abundance among different habitats. Kruskal–Wallis was also used to test for variations among habitats and seasons using R software.

Results

Trap success, species composition and distribution

A total of 887 small mammal individuals belonging to 20 species were captured in 28 224 trap nights with 3.1% trap success between July 2018 and June 2020. Closed woodland recorded the highest (6%) trap success whereas forest and the perennial riverine forest/thicket had the least with 1%. Species accumulation curves suggest the sampling effort to be adequate for three habitats (CLW, FOR and SRF), whereas for perennial riverine forest still some effort was needed (Figure 2). The asymptote for the three habitats was reached at approximately 100 individuals. The bootstrap analysis estimated a total of 21 (SD = 2) species in the northern NNP (SD = 2), whereas the Jackknife analysis estimated a maximum of 24 (SD = 4.5) species.

Overall, 91.8% of all trapped small mammals were rodents, and other groups were comprised of Macroscelidea (3.9%), Carnivores (2.4%) Eulipotyphla (1.6%), and Primates (0.3%). *Acomys ngurui* (36%) and *Aethomys chrysophilus* (17%) were the most captured species comprising 53% of all captured small mammals (Table 1). *Galerella sanguinea*, *Rattus rattus, Helogale parvula*, and *Atilax paludinosus*, were the least captured species with ≤0.2% (Table 1). Closed woodland recorded the highest species composition (53%), whereas PR had the least (7%) (Table 1).

On distribution, *A. ngurui* and *L. rosalia* were the most captured species in all habitats (Table 2). Although *A. paludinosus, Cricetomys ansorgei, R. rattus, H. parvula* and *Mungos mungo* were restricted in one habitat (seasonal riverine forest) (Table 2).

Acomy ngurui abundance

Acomys ngurui abundance was significantly different ($\chi^2 = 12$, df = 3, $p = 0.007$) between the four habitats being higher in seasonal riverine forest than in the other three habitats (Figure 3). However, its abundance was not significantly different ($\chi^2 = 2$, df = 2, $p = 0.367$) between seasons although being higher in the wet seasons (Figure 3). There was a significant difference in *A. ngurui* abundance between habitats across season ($\chi^2 = 8.2$ df = 3, $p = 0.04$).

Species richness, diversity and evenness

Seasonal riverine forest recorded the highest species richness (17), compared with other habitats (Table 3). Overall, there was no statistically significant differences in species richness between habitats across seasons ($\chi^2 = 7$, df = 3, $p = 0.071$) (Table 3). On diversity, FOR recorded the highest species diversity ($H' = 2.065$) and PR had the least ($H' = 1.506$) (Table 3). The dry season (July–October) had the highest species diversity ($H' = 1.65$), compared with short rains (November–February) and wet (March–June) seasons. Evenness was high in PR (75%), as a result of low trap success, whereas in other habitats it was low especially in SRF, where, *A. ngurui* dominated the catch, consequently affecting evenness (Table 3).

Community's similarity and small mammal habitat association

The Bray–Curtis similarity index generated four clusters of small mammal communities with a cluster accuracy of 95%. The highest similarity (85%) was recorded between perennial riverine sites 1 and 2 (PR 1 and 2; Figure 4). A second cluster was formed by forest sites 1 and 2 (FOR 1 and 2) with a similarity of 70%, whereas the third cluster is between closed woodland site 1 (CLW 1), seasonal riverine forest sites 1 and 2 (SRF 1 and 2) with a similarity of 53%. The fourth cluster was closed woodland site 1 (CLW 1), which was isolated from other clusters especially closed woodland site 2 (CLW 2), which was closely similar to those in seasonal riverine site 1 and 2 (SRF 1 and 2).

The selected variables using principle components were able to explain the habitat variation by 82.3%. PCA 1 was positively correlated with shrub, grass and canopy cover, whereas it was negatively correlated with leaf litter and number of trees. This means the areas with high grass cover and shrub diversity were CLW. PCA 2 was positively correlated with tree density, leaf litter and shrub cover and negatively associated with grass cover. These areas are seasonal riverine and forest habitats and the two habitats were relatively identical (Figure 5). Small mammal species showed different habitat preferences. *Genetta genetta* was isolated from all other species and was associated with perennial riverine forest/thickets, whereas herbivore-murids were associated with closed woodland, which is ideal for most of these species (Figure 5). *Aethomys chrysophilus* was associated with closed woodland, whereas *L. rosalia*, *M. minutoides*, *P. flavovittis, P. tetradactylus* were associated with forested areas. The rest of small mammals were associated with forest and seasonal riverine forests (Figure 5).

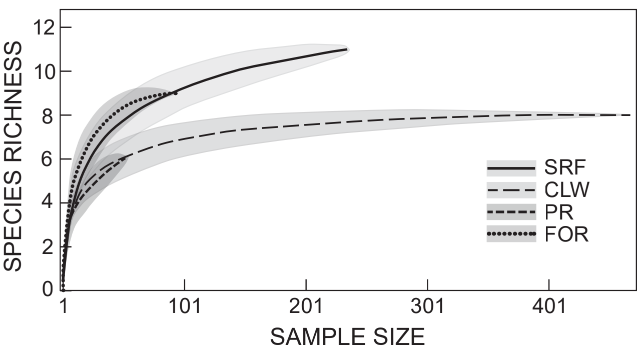

Figure 2: Species accumulation curve of small mammals in different habitats in the Selous ecosystem, Tanzania. (SRF = Seasonal riverine forest, CLW = Closed woodland, PR = Perennial riverine forest/thicket and FOR = Forest)

Discussion

Trap success, species composition and distribution

Throughout the study, the trap success was low, compared with other studies on small mammals in the areas outside protected areas (PAs). This might be attributed to low population densities especially considering the observed overall nature of the area, which is mostly dry and associated with various forms of disturbances, including prescribed burning and large herds of herbivores, in particular buffaloes. However, low catch within PAs has been attributed to high predation and large mammals grazing, compared with areas outside these PAs (Caro 2001 2002). Frequency of disturbance especially by large herds of herbivores (buffaloes) observed in the area could influence the vegetation and consequently small mammal densities (Mulungu et al. 2008). According to Hoffman and Zeller (2005), large mammal activities influence small mammal distribution through removal of cover, food and competition. Other factors include unstable food supply in the PAs and resource competition with large herbivores (Caro 2001; Zeller 2005; Ogada et al. 2009). Predators, including hyenas and leopards, were observed, whereas four different mongooses and *Genetta genetta* were captured.

Table 1: Species composition and percentage contribution (in parentheses) of small mammals in different habitats in Selous ecosystem. (CLW = Closed woodland, FOR = Forest, PR = Perennial riverine forest/thicket and SRF = Seasonal riverine forest)

sn	Species	Habitats				
		CLW	FOR	PR	SRF	Total
1	*Acomys ngurui* Verheyen et al. 2011	149 (32%)	31 (32%)	14 (24%)	126 (48%)	320 (36.08%)
2	*Aethomys chrysophilus* de Winton, 1897	131 (28%)	4 (4%)	16 (28%)	0	151 (17.02%)
3	*Mastomys natalensis* Smith, 1834	89 (19%)	12 (13%)	0	29 (11%)	130 (14.66%)
4	*Lemniscomys rosalia* Thomas, 1904	67 (14%)	2 (2%)	17 (29%)	21 (8%)	107(12.06%)
5	*Petrodromus tetradactylus* (Peters, 1846)	15 (3%)	13 (14%)	0	4 (2%)	32 (3.60%)
6	*Crocidura hitra* Peters, 1852	1 (0.2%)	2 (2%)	0	19 (7%)	22 (2.48%)
7	*Paraxerus palliatus* (Peters, 1852)	0	6 (4%)	0	16 (6%)	22 (2.48%)
8	*Mus minutoides* Smith, 1834	11 2%)	8 (8%)	0	0	19 (2.14%)
9	*Paraxerus flavovittis* (Peters, 1852)	4 (1%)	0	3 (5%)	11 (4%)	18 (2.03%)
10	*Cricetomys ansorgei* Thomas, 1904	0	0	0	15 (6%)	15 (1.69%)
11	*Beamys hindei* Thomas, 1909	0	10 (10%)	0	3 (1%)	13 (1.47%)
12	*Grammomys surdaster* Thomas and Wroughton 1908	0	4 (4%)	2 (3%)	7 (3%)	13 (1.47%)
13	*Genetta genetta* (Linnaeus, 1758)	0	1 (1%)	6 (10%)	0	7 (0.79%)
14	*Grammomys selousi* Denys et al. 2011	0	2 (2%)	0	3 (1%)	5 (0.56%)
15	*Mungos mungo* (Gmelin, 1788)	0	0	0	3 (1%)	3 (0.34%)
16	*Otolemur garnetti* (E. Geoffroy 1812)	0	2 (2%)	0	1 (0%)	3 (0.34%)
17	*Atilax paludinosus* F. Cuvier 1826	0	0	0	2 (1%)	2 (0.23%)
18	*Helogale pervula* Sundevall 1847	0	0	0	2 (1%)	2 (0.23%)
19	*Rattus rattus* Linnaeus, 1758	0	0	0	2 (1%)	2 (0.23%)
20	*Galerella sanguinea* Ruppell 1836	0	0	0	1 (0%)	1 (0.11%)
	Total	467 (100%)	97 (100%)	58 (100%)	265 (100%)	887 (100%)
	Habitat contribution	53%	11%	7%	30%	
	Species richness	8	13	6	17	

Table 2: Small mammal species distribution in different habitats in Selous ecosystem, Tanzania. (CLW = Closed woodland, FOR = Forest, PR = Perennial riverine forest/thicket and SRF = Seasonal riverine forest)

Species	Habitats			
	CLW	FOR	PR	SRF
Acomys ngurui Verheyen et al. 2011	×	×	×	×
Aethomys chrysophilus de Winton, 1897	×	×	×	
Atilax paludinosus F. Cuvier 1826				×
Beamys hindei Thomas, 1909		×		×
Cricetomys ansorgei Thomas, 1904				×
Crocidura hitra Peters, 1852	×	×		×
Galerella sanguinea Ruppell 1836				×
Genetta genetta (Linnaeus, 1758)		×	×	
Grammomys surdaster Thomas and Wroughton 1908		×	×	×
Grammomys selousi Denys et al. 2011		×		×
Helogale pervula Sundevall 1847				×
Lemniscomys rosalia Thomas, 1904	×	×	×	×
Mastomys natalensis Smith, 1834	×	×		×
Mungos mungo (Gmelin, 1788)				×
Mus minutoides Smith, 1834	×	×		
Otolemur garnetti (E. Geoffroy 1812)		×		×
Paraxerus flavovittis (Peters, 1852)	×		×	×
Paraxerus palliatus (Peters, 1852)		×		×
Petrodromus tetradactylus (Peters, 1846)	×	×		×
Rattus rattus Linnaeus, 1758				×

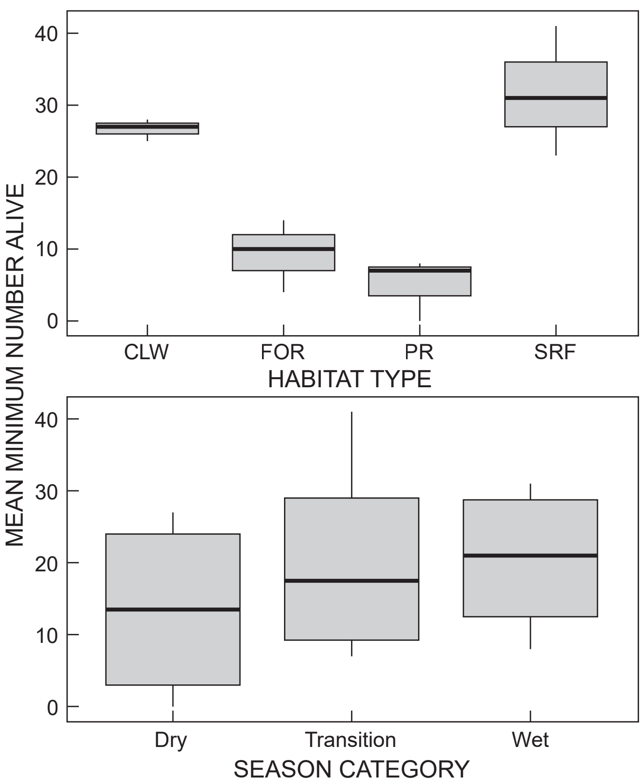

Figure 3: *Acomys ngurui* abundance in different habitats (a) and seasons (b) in Selous ecosystem, Tanzania. (SRF = Seasonal riverine forest, CLW = Closed woodland, PR = Perennial riverine forest/thicket and FOR = Forest)

High capture in closed woodland was a result of four dominant small mammal species; *A. ngurui*, *M. natalensis, L. rosalia and A. chrysophilus.* High catch of these species might be caused by effects of prescribed burning on pasture that is suitable for herbivore murids (Namukonde and Simukonda 2018). In addition, these areas were higher, compared with other habitats, which affirms the theory that higher areas like mountains are good habitat for small mammals during harsh climates (Mulungu et al. 2008). Population fluctuation was observed in closed woodland suggesting an effect of habitat changes with season, prescribed burning effects and large herbivore activities. Low catch recorded in perennial riverine forest/ thickets was possibly because of sparse undergrowth, which might affect food and shelter, which are key to small mammal survival. This is in line with reports by various authors (Monadjem and Perrin 2002; Makundi et al. 2005; Mulungu et al. 2008; Venance 2009; Mohammadi 2010), that environmental factors can shape coexisting species differently depending on localities and seasons, consequently affecting their occurrence and fluctuation in a given habitat. For example, some species might have died, because of erratic runoffs caused by heavy rain and presence of water lodged areas.

On distribution, *A. ngurui* and *L. rosalia* were captured in all four habitats. The genus *Acomys* has been reported to be widely distributed in tropical Africa (Mbugua 2002; Kingdon 2015). However, Venance (2009) reported the species to be restricted to one habitat (Acacia-Dalbergia woodland), which was possibly caused by sampling intensity. *Lemniscomys rosalia* is established in the ecosystem and well adapted to prescribed burning, a common management phenomenon in most tropical African PAs characterised by miombo woodland. In addition, fire does not affect survival of this species

Table 3: Species richness and diversity of small mammals in Selous ecosystem, Tanzania. (CLW = Closed woodland, FOR = Forest, PR = Perennial riverine forest/thicket and SRF = Seasonal riverine forest)

Habitat/Seasons	Richness	Simpson (1–D)	Shannon (*H*′)	Evenness (*E*)
SRF Overall	17	0.7285	1.79	0.3992
SRF Dry	10	0.7498	1.785	0.5958
SRF Wet	10	0.7324	1.703	0.5492
SRF short rain	10	0.6859	1.566	0.4785
CLW Overall	8	0.7616	1.572	0.6020
CLW Dry	5	0.7340	1.382	0.7970
CLW Wet	8	0.7198	1.457	0.5366
CLW short rain	8	0.7775	1.645	0.6475
PR Overall	6	0.7464	1.506	0.7515
PR Dry	4	0.6942	1.264	0.8846
PR Wet	4	0.5455	1.034	0.7028
PR Short rain	5	0.6961	1.323	0.7508
FOR Overall	13	0.8291	2.065	0.5630
FOR Dry	12	0.8512	2.17	0.7299
FOR Wet	7	0.7469	1.586	0.6975
FOR Short rain	9	0.7910	1.829	0.6919

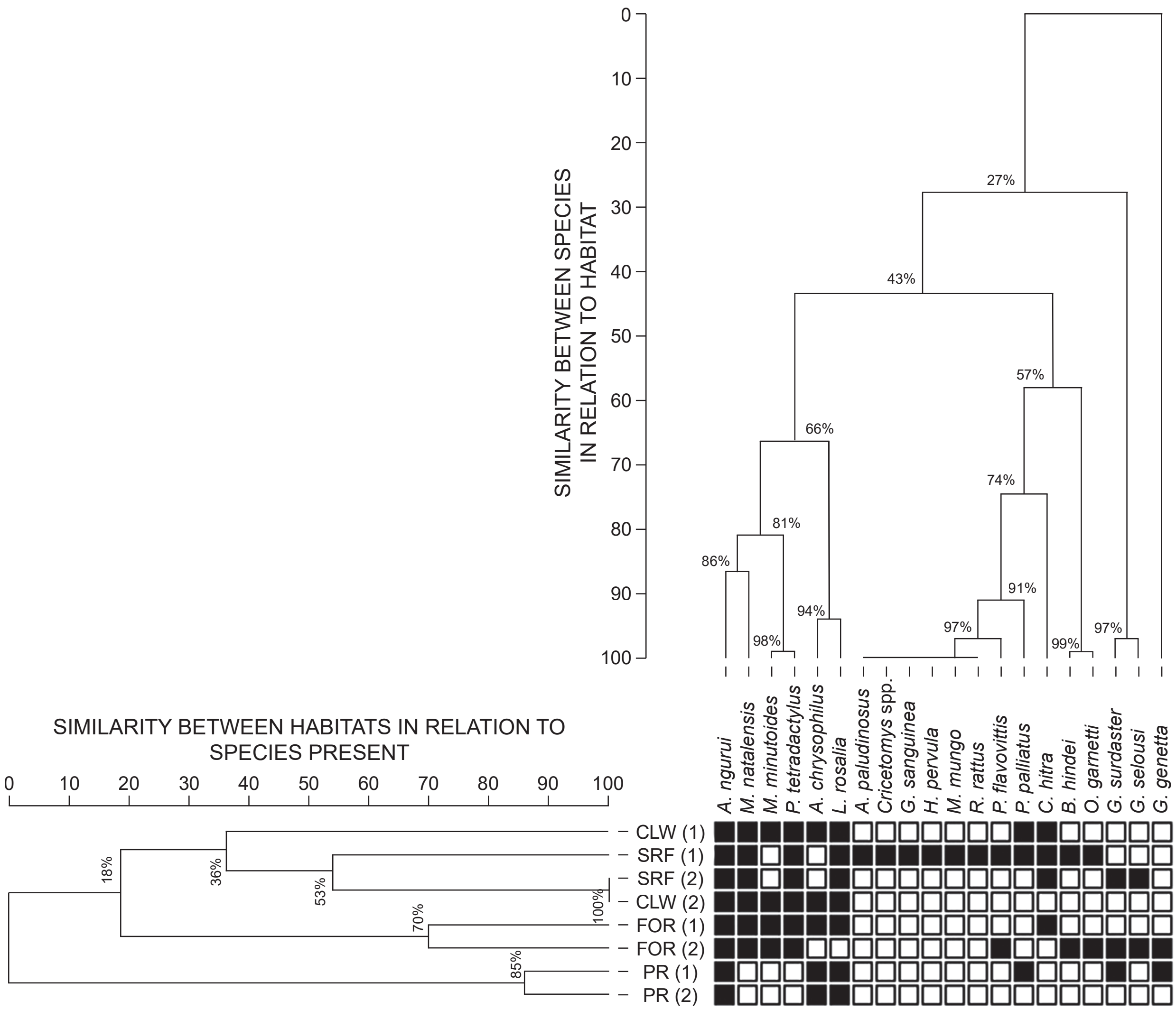

Figure 4: Hierarchical clustering dendrogram from the Bray–Curtis similarity analysis of small mammals' communities and species in Selous ecosystem, Tanzania. Boxes indicate the presence or absence of species (SRF = Seasonal riverine forest, CLW = Closed woodland, PR = Perennial river forest/thicket and FOR = Forest)

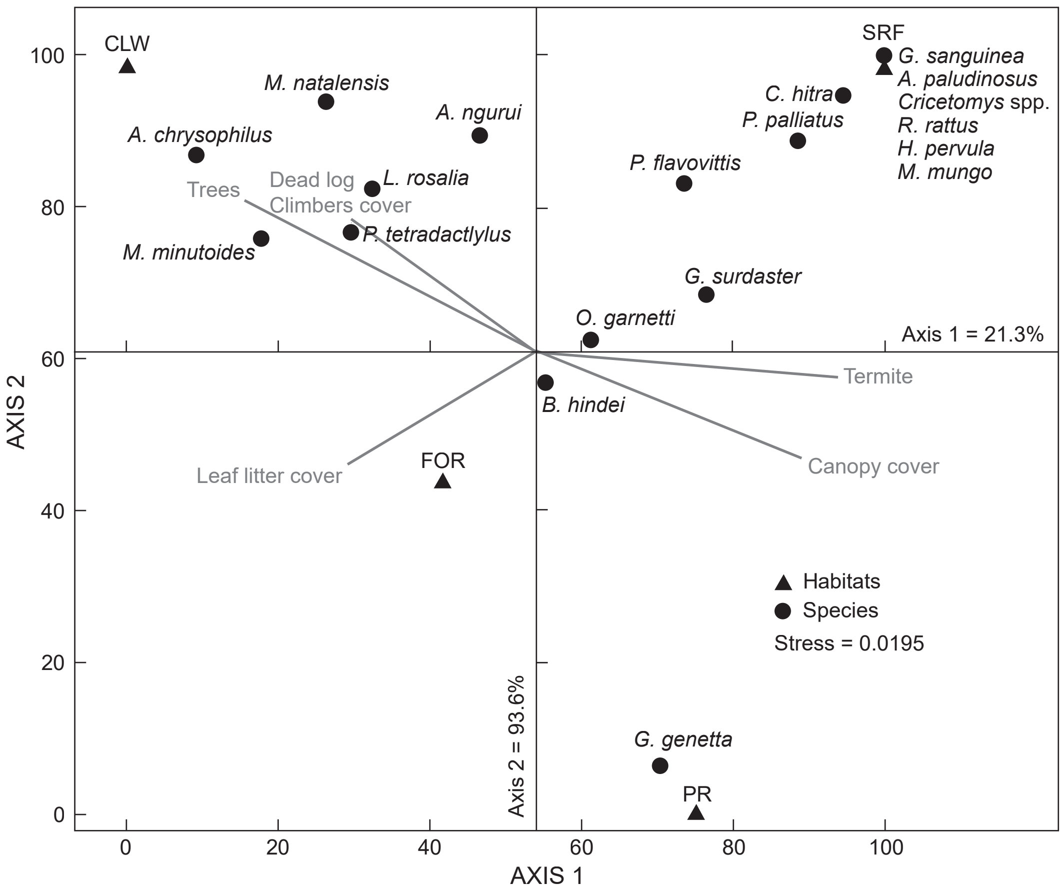

Figure 5: Non-Metric Multidimensional Scaling (NMDS) on small mammal–habitat association. SRF = Seasonal riverine forest, CLW = Closed woodland, PR = Perennial riverine forest/thicket and FOR = Forest

and they tend to change their home ranges and activity patterns to accommodate its effects (Kingdon 1997; Monadjem and Perrin 1997; Yarnell et al. 2008). On the other hand, *M. natalensis* appeared in late September 2018 in closed woodland after a prescribed burning incidence and dominated the catch in this habitat until January 2019. Its occurrence after fire affirms that this species recolonises after a disturbance (Monadjem and Perrin 2002; Massawe et al. 2005; Massawe et al. 2008). However, its density decreased with increasing vegetation cover in the wet season. To the contrary, as *M. natalensis* catch decreased, *A. chrysophilus* and *L. rosalia* dominated the catch during this time suggesting a variation in habitat suitability by seasons among these murid species.

Rattus rattus, A. paludinosus, *G. sanguinea* and *C. ansorgei* were the least occurring species in this study. Restriction of *Cricetomys ansorgei* to seasonal riverine forest is contrary to Kingdon (2015), who suggested they vary extensively in their habitats. A possible reason for its occurrence may be habitat suitability in seasonal riverine forest, which is characterised by sandy-loamy soils in most areas and dense vegetation and associated with human activity (rangers' base camp). The other three habitats are mainly rocky areas and might not support this species especially considering their requirement of extensive burrows (Kingdon 2015). *Genetta genetta* occurred in forest and perennial riverine forest/thickest might be associated with its territorial, solitary and semi-arboreal life, for which the two habitats are suitable (Amroun et al. 2014).

Grammomys selousi is reported for the first time in the northern part of Rufiji River. This species was first reported by Denys et al. (2011) in the southern part of Rufiji River in Kichi Coastal Forest and since then there have been no further records for this species from this area. The species was captured in all four habitats in which *G. surdaster* was captured. The presence of this species in the northern part of Rufiji River suggests that the species is a common resident in the entire northern part of the Selous ecosystem, necessitating an additional study on this species and its relative *G. surdaster*.

Acomys ngurui abundance

Acomys ngurui was the most captured species in this study. The high catch of *A. ngurui* can be explained by a dry and hot habitat with rocky outcrops, which is suitable for this species (Ogada et al. 2009; Kingdon 2015). Low abundance in perennial riverine forests was possibly caused by sparse undergrowth. High abundance of *A. ngurui* in the wet season affirm the effects of rainfall on rodent species abundance through increased food and cover (Alemayehu and Bekele 2013; Bantihun and Bekele 2015). In all habitats, *A. ngurui* abundance was higher in January 2019 and, except for seasonal riverine forests, abundance was also higher in January 2020, suggesting consistent patterns in the three habitats. In general, although no statistically significant, variation was noted there was a fluctuation in abundance in the four habitats evident in January following the short rains and May, which marks the end of the wet season. Variation in abundance fluctuation in each habitat suggests a possible varied effect resulting from different environmental factors, such as cover, predation, food and competition, as reported by Makundi et al. (2005). The occurrence of this species in such high numbers in the four habitats suggests a possibility that, there might be more than one species of *Acomys* in this area.

Species richness and diversity

The observed high richness and diversity in the seasonal riverine forest and forest habitat can be explained by availability of cover and food, which are reported to determine the level of competition and niche differentiation. The niche theory suggests that different species are confined in their specific niche and are limited by different environmental factors, consequently allowing coexistence (Hubbell 2001; Tews et al. 2004; Stein et al. 2014). In addition, various authors have pointed out that floristic diversity, spatial and temporal heterogeneity and habitat complexity in a given habitat influence food and shelter and therefore species occurrence (MacArthur and MacArthur 1961; Wright 2002; Makundi et al. 2005; Mukinzi et al. 2005; Mulungu et al. 2008; Elmouttie 2009; Venance 2009; Yihune and Bekele 2012). The habitat complexity provides species with variable feeding options that are necessary in energy reduction in foraging (Elmouttie 2009; Garshong et al. 2013). Low diversity in perennial riverine forest/thickets could be because of the nature of the area (a cliff riverine with rock outcrops in most areas and sparse undergrowth and frequent disturbances from large herbivores mainly buffalos). Low diversity in closed woodland was caused by occurrence of four dominant species i. e. *A. ngurui, L. rosalia, A. chrysophilus* and *M. natalensis*, which affected evenness, compared with other habitats.

Seasonal effect on diversity was notable in seasonal riverine forest and perennial riverine/thickets habitats, which recorded only one species (*A. ngurui*) in May 2019, possibly because of heavy rainfall between March and June 2019, therefore affecting the species diversity. Transition period recorded the highest species diversity in the three habitats except in seasonal riverine forest suggesting this season to favour small mammals in the ecosystem. The difference observed in seasonal riverine forests might be because of vegetation cover hence food supply in a small area. In addition, there were no erratic runoffs in the wet season, which might impose direct mortality to small mammals, as observed in closed woodland and perennial riverine/thickets habitats. Low number of individuals might also be the reason for low trappability and consequently affecting diversity. Another possible reason that might affect diversity can be reduced home ranges, because of resource availability in a smaller area in the wet season, as pointed out by Borremans (2013) and therefore affecting trappability. However, these results are contrary to what was reported by Assefa and Srinivasulu (2019).

Community's similarity and small mammals' species habitat association

Most species in this study were associated with closed woodland and seasonal riverine forest. Most murids, except *Rattus rattus* were associated with closed woodland, which was characterised by tall grass cover an ideal habitat for both shelter and food for murids. The occurrence of *R. rattus* in the seasonal riverine forest can be explained by association with human where this area is close to the main ranger's camp in the Selous ecosystem. These two habitats were relatively complex in terms of vegetation cover and microhabitats, which were possibly the factor for preference of more species. According to Mukinzi et al. (2005), a complex habitat will provide for niche separation and hence reduced competition in relatively small areas, because of availability of constant food supply and shelter. Liu et al. (2018) reported that species will be successful in a given habitat in terms of dominance and abundance only if it associates well with its habitat. This means, it will be able to competitively dominate the area over other species or coexist. Species usually coexist through evolution by occupying different resources through time and space, which is a driver for species habitat association (Chuyong et al. 2011). A few species, including *B. hindei, G. surdaster*, *G. selouis* and *O. garnetti* are likely to be habitat generalist, because they occurred almost at the center of all habitats. Another species with a different distribution was *G. genetta*, although captured in more than one habitat and a carnivore, which was expected to associate with murid species as a predator, associated with perennial riverine forest/thickets suggesting a preference to other sources of food other than small mammals.

Conclusions and recommendations

This study has provided an update on the distribution of small mammals, with the report of a new population of murid (*Grammomys selousi)* in the northern part of the Rufiji River. In addition, this study shows that the small mammal species abundance, diversity and distribution are largely influenced by habitat types and seasonal variations. This study further suggests that management actions, including prescribed burning, infrastructure development and general management plans (GMP), should be updated to include the distribution of small mammals in the park. In addition, considering the importance of this component to the ecosystem, additional studies on small mammals are recommended in this ecosystem.

Ethical statement — This animal study was reviewed and approved by Sokoine University of Agriculture (SUA) via Permit Number: SUA/ADM/R.1/8/204 dated May 2018 and Tanzania Wildlife Management Authority (TAWA) via Permit Number: AC.517/625/01.

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