Original Research Article

Land use and habitat selection by small mammals in the Tanzanian Greater Serengeti Ecosystem

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ABSTRACT

Habitat selection is central to shaping the abundance and distribution of organisms in space and time. We analysed land use (National Park, pastoralism and agriculture) and habitat selection by small mammals in the Tanzanian Serengeti Ecosystem, and how selection varies with rainfall seasonality and characteristics of used microhabitats. We trapped 612 small mammals in five habitat types distributed over the three land uses in the wet and dry seasons. The majority of the nine commonest species selected at least two of the three land uses and several habitat types, indicating wide distribution in the ecosystem. *Crocidura* spp., *Dendromus melanotis*, *Graphiurus murinus*, *Mus sorella* and *Mus* sp. selected the more intact and least disturbed National Park and apparently avoided the disturbed pastoral or agricultural lands while *Aethomys* sp., *Arvicanthis niloticus*, *Gerbilliscus vicinus* and *Mastomys natalensis* mainly selected the pastoral and agricultural lands. Land use and habitat selection patterns were consistent between seasons for four species. Thus, *D. melanotis*, *G. murinus*, *Crocidura* spp. and *Mus* sp. selected the park in both seasons but had lower relative abundances in the dry season. Pest and opportunistic species that prefer seeds mainly selected either the shrubland and cropland in both seasons (*A. niloticus* and *G. vicinus*), or the cropland in both the pastoral and agricultural lands but had higher relative abundances in the dry season (*Aethomys* sp. and *M. natalensis*). Most habitat specialists selected the park, which comprised of more diverse and less disturbed habitats. In contrast, generalist and pest species selected the disturbed pastoral and agricultural lands, implying that intensifying human activities near protected area edges favor opportunistic and pest species less sensitive to disturbance. These findings show that human disturbance alters ecological communities, impoverishing them by displacing specialist species to the benefit of pest species, which, in turn, may negatively affect human activities and livelihoods.

1. Introduction

Habitat selection is a crucial process in the life cycle of animals because it affects most components of their ecology, fitness and survival (Danchin et al. 1998, Resetarits and Binckley, 2009). It is the process by which individual animals choose among available habitats (Mohammadi, 2010) and is manifested in disproportionate use of particular habitat types (Johnson, 1980,

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Rosenzweig, 1981). Knowledge of habitat selection is central to understanding mechanisms shaping the distribution and abundance of animals in space and time (Hodara and Busch, 2010), but it can be exceedingly hard to assess selection (Otis, 1997). This is because multiple factors influence habitat selection, including habitat type, structure and quality. These factors collectively determine habitat suitability that encompasses availability of shelter, food and nesting sites, presence of competitors, predation risk, parasites and disease prevalence (Torre and Díaz 2004, Hodara and Busch, 2010, Sponchiado et al. 2012). Additional factors that affect habitat selection include life-history traits and strategies, such as dispersal ability (Silva et al. 2005), evolutionary history, degree of specialization of a species (Torre, 2004) and environmental seasonality. Notably, rainfall seasonality affects habitat selection through its influence on habitat structure and quality (Martín and López 1998, Bantihun and Bekele, 2015). Consequently, species differ in their habitat selectivity and perception of the scale and degree of habitat heterogeneity (Coppeto et al. 2006). Understanding habitat selection can therefore inform many decisions in species conservation and management, such as identifying populations requiring priority conservation attention (Hebblewhite and Haydon, 2010), translocations, habitat restoration or rewilding (Miller and Hobbs, 2007, Stamps and Swaisgood, 2007, Schweiger et al. 2019).

It follows that factors and processes that alter natural habitat heterogeneity also modify habitat selection. Accordingly, anthropogenic activities, that modify natural habitat heterogeneity, also alter habitat selection, including by small mammals. Such alteration to natural habitats can occur in multiple ways. For example, agriculture can influence small mammal populations by simultaneously providing them with abundant food while also homogenizing their habitats (Caro, 2001, Michel et al. 2006). Moreover, livestock pastoralism can promote vegetation regrowth and enhance nutrient flow but also accentuate mechanical disturbance to vegetation, reduce plant biomass and alter vegetation composition (Schmidt et al. 2005). As a result, land use ranks among the leading conservation concerns as it degrades natural habitats, create and sustain hard edges between protected areas and their surrounding human-dominated landscapes (Ogutu et al. 2005, Hurst et al. 2013). Wildlife species respond contrastingly to land use with some benefitting whereas others are disadvantaged (Geier and Best, 1980, Datiko and Bekele, 2013). Such interspecific distinctions, including in microhabitat selection, have been observed among sympatric small mammal species responding to land use changes (Eccard et al. 2000, Blaum et al. 2007, Byrom et al. 2015).

For small mammals, interspecific differences in characteristics associated with habitat selection, such as habitat utilization (Vieira and Monteiro-Filho, 2003, Oliveira-Santos et al. 2008), peak activity periods (Oliveira-Santos et al. 2008) and food requirements (Cáceres et al. 2002), enable sympatry or co-existence. Interspecific differences in habitat selection by small mammals are therefore vital in enabling multiple species to coexist (Dalmagro and Vieira, 2005, Traba et al. 2010, Novillo et al. 2017). Coexistence is also possible because species differ in the frequency with which they use specific habitats and how they perceive microhabitat quality (Garshelis, 2000, Dalmagro and Vieira, 2005, Sponchiado et al. 2012). As a consequence, how small mammals respond to habitat changes can be predicted from changes in habitat characteristics (Murúa and González 1982).

Given the centrality of habitat selection in animal ecology, it is crucial to advance our understanding of how small mammals respond to anthropogenic land use. Small mammals are ideal subjects for studying how animals respond to land use and habitat selection because of their small body size and small home ranges (Hodara and Busch, 2010). In addition, they respond strongly to spatial habitat gradients (Sauvajot et al. 1998). Here, we examine land use and habitat selection by small mammals by relating relative abundance to land use, comprising protection in a National Park, livestock pastoralism and crop agriculture, and habitat type in each land use, and characteristics of selected microhabitats in each habitat type. We thus treat selection as a hierarchical process and assess it at three nested levels: land use, habitat types nested within land use and microhabitats nested within habitat types. Moreover, we examine how land use and habitat selection patterns vary between the wet and dry seasons.

We test two hypotheses; H_1) Small mammals differ in their preferred habitats, and H_2) Land use and habitat selection vary seasonally. From these we derive four predictions; P_1) Most small mammal species select the National Park and the habitats in it and they avoid the more disturbed agricultural land more than the relatively less disturbed pastoral land. P_2) The pest species will be the most common species in the agricultural land, they will be intermediate in the pastoral land, and the least common in the protected park. P_3) Most species select less disturbed (more intact and safer) habitats in the National Park, especially in the peak breeding (wet) season. P_4) The pest species select the agricultural land during the harvesting period (dry season) when food quality and abundance peak.

2. Materials and methods

2.1. Study area

The study was carried out in the Greater Serengeti Ecosystem in northern Tanzania, East Africa. We focused on the northeastern section of the Serengeti Ecosystem, including the Serengeti National Park (2° 20′ S, 34° 50′ E) and two adjacent districts, namely the Serengeti (2°15′ S, 34°68′ E) and Ngorongoro (3°24′ S, 35° 48′ E). The Serengeti National Park protects 14,750 km^2 of tropical savanna ecosystem (Sinclair, 2008). The park encompasses woodlands, wooded and open grasslands and other more restricted habitat types (Reed et al. 2009, Byrom et al. 2014), with farming and livestock herding practiced around the ecosystem. The climate in the ecosystem is warm and dry, with mean temperatures ranging between 15 and 25 °C (Magige, 2016). The rains are bimodal with the short rainy season spanning November–January and the long rainy season covering March – May (Norton-Griffiths et al. 1975). Rainfall increases in the ecosystem from the east to the west towards Lake Victoria (Sinclair, 1995) and along a gradient from the dry south-eastern plains (700 mm/year) to the wet north-western region (1050 mm/year). Long-

term data obtained from the Tanzania National Parks (TANAPA) showed that the total monthly rainfall averaged 78 mm, whereas temperatures averaged 26 °C during the study period.

2.2. Study design

The study was carried out within three contrasting blocks located along the Mto Wa Mbu-Musoma road traversing the northern part of the Serengeti Ecosystem in the wet (April and May) and dry (August and September) seasons of 2017 and 2018. The area was chosen because it has contrasting land use types, including agricultural land (south west), pastoral and agricultural lands in the south east and the Serengeti National Park, located between the two land use types (Fig. 1). Each of the three blocks was partitioned into four plots using general vegetation characteristics for a total of 12 plots ("habitats"). However, only 10 habitats were included in the study because two habitats (wooded grassland and grassland in the pastoral land) are situated in a pastoralist village, Ololosokwan, with a long-standing land use conflict with TANAPA. As a result, we visited the latter two habitats only once and were denied permission for further visits. Consequently, the two habitats in Ololosokwan were excluded from this study.

The 10 habitats belonged to five habitat types, four in the Serengeti National Park (wooded grassland, shrubland, grassland and riverine forest), four in the agricultural land (wooded grassland, shrubland, grassland and cropland) and two in the pastoral land (shrubland and cropland). The cropland habitat type was represented by maize and bean farms. In addition to the rainfall data provided by TANAPA, the habitats had contrasting surface air temperatures and humidity. These were measured in each habitat twice daily, in the morning and evening, 1 m above the ground level, using Oregon Scientific THGR810 10-Channel Wireless Remote Thermometer/Humidity Sensor. Rainfall and humidity were higher in the pastoral land than in either the park or agricultural land and; higher in the wooded grassland and riverine forest than in the other habitats in the park. Humidity was higher in the agricultural land than in the park, especially in the wet season, except for the grassland habitat. Humidity was also higher in the wet than the dry season in all the other habitats regardless of land use (Table S1).

2.3. Trapping small mammals

Traps were set on a 100 × 100 m (1 ha) grid in each habitat (plot). To maximize trapping of small mammals, we used three trap types, Sherman traps, wire mesh and bucket pitfall traps. A total of 141 traps (100 Sherman traps, 30 wire mesh and 11 bucket pitfall traps) were used. The wire mesh traps (*mgono*) are multiple capture live-traps with a 'one-way' entrance that allows small mammals in but not out. The most common entrance of this kind is funnel shaped. These traps are typically made of thin wire and are widely used in Tanzania by local hunters. Traps were set in each plot for five consecutive nights and then transferred to the next plot for a further five consecutive nights.

Each plot had one pitfall line with 11 buckets, spaced 5 m apart, and buried into the ground such that the top of the bucket was at the ground level. The layout of the pitfall traps followed Stanley et al. (2011). This technique has been used with success in other small mammal surveys, especially for capturing shrews (*Crocidura* spp.) and other low-weight species (Stanley and Hutterer, 2007, Stanley et al. 2011). This is a passive and non-baited trapping procedure that captures mainly animals moving along the drift fence on the habitat floor until they fall into a bucket. Although pitfalls were set in straight lines, rocks and logs caused occasional deviations. For the Sherman traps (23 × 9.5 × 8 cm), we developed 10 lines (10 m apart) on the grid and arranged the traps along the line, 10 m apart from one trapping station to the next, for a total of 100 Sherman traps per 100 × 100 m plot. A total of 30 wire mesh traps were placed together with the Sherman traps such that both trap types occurred at each of the 10 trapping positions in the 3rd, 6th and 9th columns of the trapping grid row (Fig. 2). We baited both the Sherman and "*mgono*" traps using fresh fried coconut coated with peanut butter and mixed with Lake Victoria sardines (*Rastrineobola argentea*). The traps were rebaited every day in the morning between 6:30–8:30 am and late afternoon between 17:00–19:00 pm. We recorded body mass and external morphometric measurements (external shape and dimensions) such as the lengths of the body, tail, ear and the hind foot of each trapped animal and identified them to the genus or species level following Kingdon (2015) and Kirsten (2009). Further, we recorded other individually distinctive features such as sex, reproductive status and presence of scars to facilitate individual identification (Graham and Lambin, 2002). To avoid multiple counts, all captured animals were marked by toe clipping using a sterilized scissor and released at the points of capture.

2.4. Measuring characteristics of used microhabitats

Structural microhabitat characteristics (environmental variables) were measured within a five-meter radius of any trapping station where at least one small mammal of any species was captured. A microhabitat thus differs from the four "habitat types", distinguished by the general vegetation type in which the trapping grid was located (forest, wooded grassland, grassland, cropland and shrubland). To characterize microhabitats, we measured 10 variables within a five-meter radius of 532 trapping stations in both the wet and dry seasons. These were the height and percent cover of grass, herbs, shrubs and trees, tree diameter at 1.5 m above ground and litter depth. Grass, herb and shrub cover were visually scored on a scale of 0–100% (Gautam et al. 2014). Although there is a narrow difference between grasses and herbs, we define grasses as long, narrow, leafy plants with sheaths while herbs are broad, leafy plants with petioles or sessiles (Lillybridge and Williams, 2002). Tree canopy cover was measured using a modified densiometer composed of a mirror divided into 24 squares each of 1 cm length and positioned about 1.5 m above the ground level. Measurements were taken at four points in each sampling unit, up to 5 m from the live trap
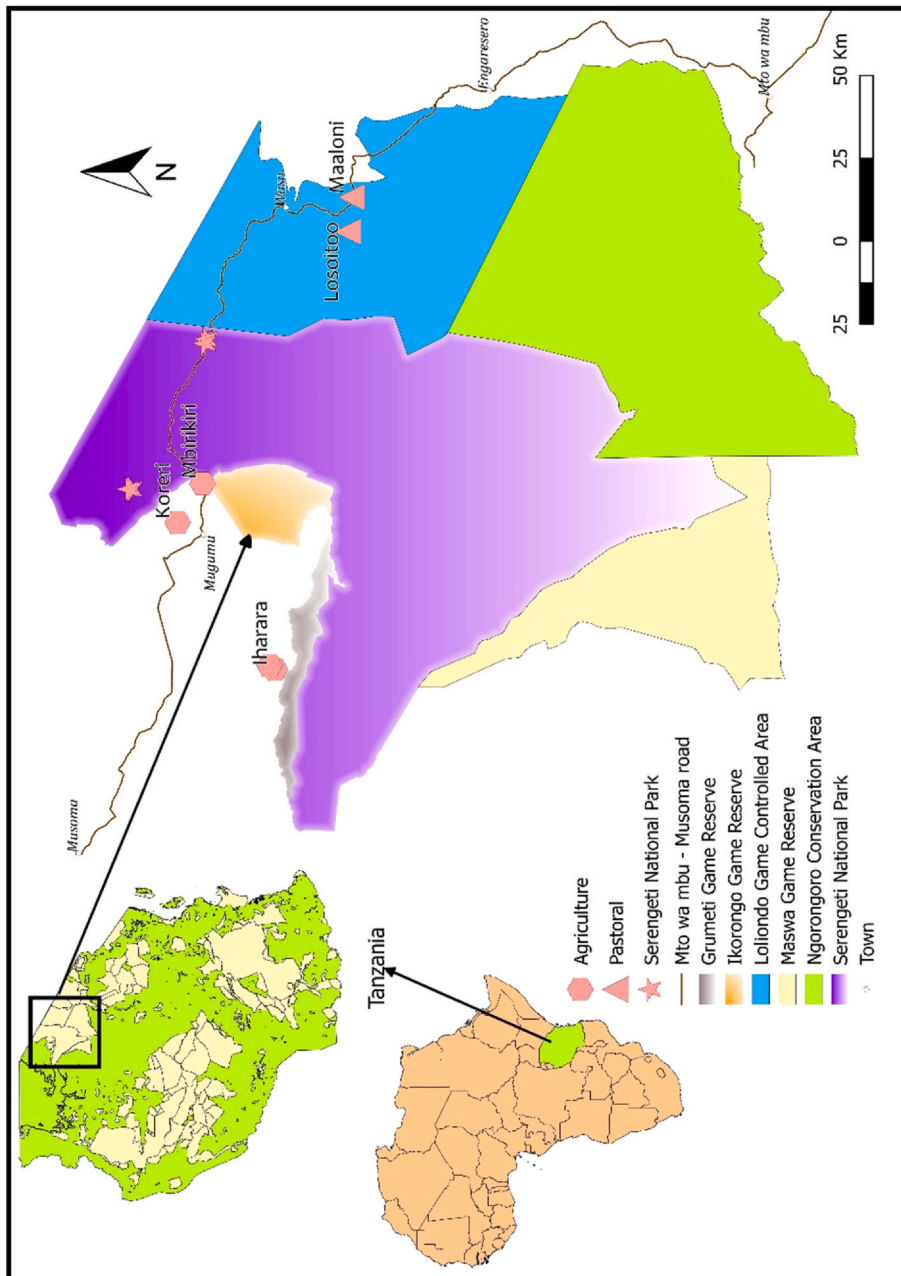
Fig. 1. Map of the Greater Serengeti Ecosystem showing the study sites (pink color) arrayed along the Mto Wa Mbu–Serengeti road.
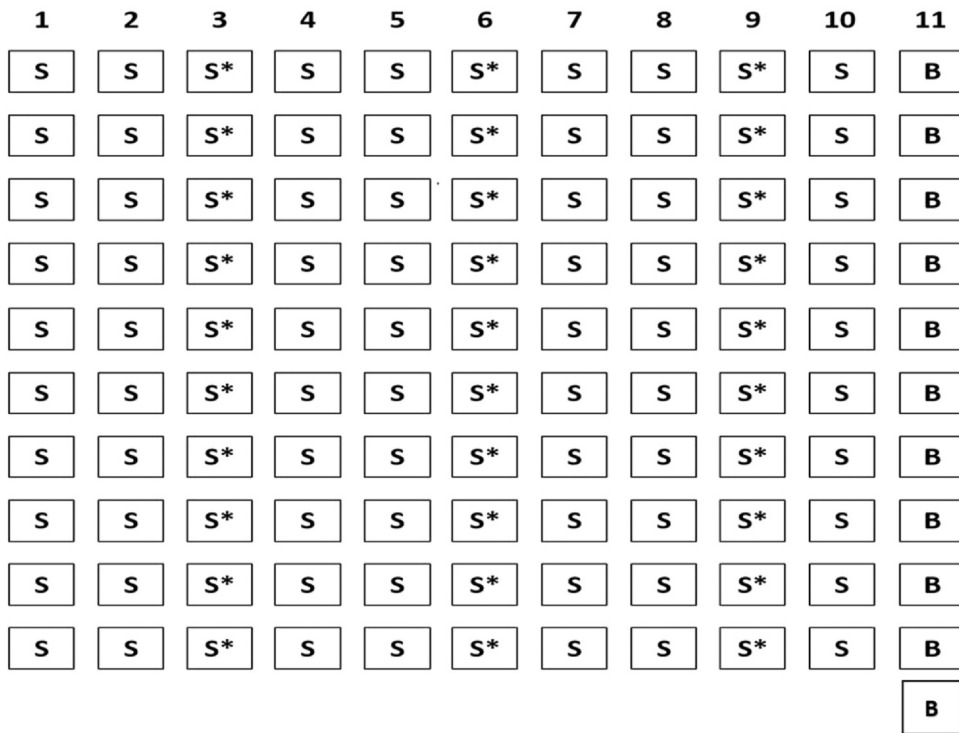
Fig. 2. Trap layout in each 100 × 100 m trapping grid in one habitat (plot) in the study ecosystem. S denotes the positions of the trapping stations with the Sherman traps only whereas S* refers to the positions of the trapping stations with both the Sherman and wire mesh traps. The bucket pit fall traps (B) were placed on either side of the plot.

along the four cardinal compass directions (north, south, east and west). The four measurements were averaged to obtain one measurement for each variable per trapping station (Comeau et al. 1998, Warren et al. 2013). Litter depth was measured with a measuring tape at the same four points in each sampling unit and averaged.

2.5. Statistical data analysis

We consider only the nine most abundant out of the total of 19 species captured, because the remaining 10 species had only 1–9 non-zero captures, which were too few to reliably analyse. The total sample size for each species was 5640 = 141 trapping stations × 10 habitats × 2 seasons × 2 years. We used the zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB) regression models, each with a log link function, to relate the counts (number of first-time captures) for each of the nine commonest species separately to land use, habitat type and season and all their possible interactions (Appendix 1).

The same effects were fitted to both the count and zero-inflation parts of the ZIP and ZINB models. The zero-inflation part of both models had a logit link function. We used automatic variable selection to independently select, for each species, the best-supported models for the count and zero-inflation parts of the models. We selected the best supported models using forward and stepwise variable selection procedures and the Akaike (AIC), corrected Akaike (AICc) and Schwarz Bayesian (BIC) Information Criteria and Wald-type Chi-square tests. Levels of the three classification variables (land use, habitat type and season) were split into multiple effects that correspond to individual levels of each variable, each of which entered or was removed from the model independently. More precisely, the columns of the design matrix that correspond to land use, habitat type or season were each selected to enter or leave the models independently of the other design columns of that effect (Appendix 1). This is equivalent to dummy coding of each level of the three classification factors. A strong hierarchy criterion or marginality constraint (Nelder, 2000) was imposed so that interaction terms were only retained if the main effects were already retained in the selected models. The models were fit using the SAS HPGENSELECT Procedure (SAS Institute 2020). The results are presented in appendices 1 and 2. Together with the results of the regression models, relative abundance was used to determine the selected land use and habitat types. Furthermore, relative abundance of small mammals was used to determine whether species abundance changed with season ("seasonal") or not ("aseasonal") as well as peak activity time (diurnal or nocturnal, Appendix 3).

The relative abundance of the small mammal species could not be related to the microhabitat variables using statistical models because the variables were not measured for all the 5640 capture stations but only for the subset of 532 stations where at least one small mammal of any species was captured. This was necessitated by logistical and other constraints but, unfortunately, resulted in incomplete data for the microhabitat characteristics. As a result, we only calculated descriptive

summary statistics for each of the 10 microhabitat variables and used these to quantitatively characterize the microhabitats used by each of the nine commonest small mammal species.

3. Results

3.1. Relative abundance of small mammals

During the 28,200 trap nights of effort, we captured a total of 682 individuals of the nine commonest species, including 114 recaptures. However, we analysed only the data for the 568 first-time captured small mammals belonging to the nine commonest species (Fig. 3). The land use and habitat type in which the small mammals were trapped, and the number trapped in each varied between species. In particular, *Arvicanthis niloticus, Mastomys natalensis* and *Crocidura* spp. were the most numerically abundant species in the ecosystem (Fig. 3). Although most species were trapped in more than one land use or habitat type, some were mostly trapped in either the pastoral land (*Arvicanthis niloticus* and *Mastomys natalensis*), National Park (*Crocidura* spp. and *Dendromus melanotis*), or agricultural land (*Gerbilliscus vicinus*) (Appendix 2, Fig. 3).

3.2. Land use, habitat selection and seasonality in selection patterns

Land use and habitat selection varied among the small mammal species (H_1) and between the wet and dry seasons. Consequently, most small mammals were captured in the pastoral land ($n = 268$), followed by the park ($n = 212$), and the least in the agricultural land ($n = 88$), but the majority of the small mammal species were trapped in the National Park (P_1). Each of the captured small mammal species used either all or two of the three land uses (Appendix 2). Only one species each was not captured either in the National Park (*G. vicinus*) or pastoral land (*D. melanotis*) whereas two species were not captured at all in the agricultural land (*A. niloticus* and *G. murinus*). Moreover, two species, *Crocidura* spp. and *D. melanotis*, showed the strongest preference for the park and, to a lesser degree, the agricultural land, but avoided the pastoral land (Fig. 4 and Appendix 2). Two more species, *Mus* sp. and *Mus sorella*, showed similar but weaker patterns, but they were widely distributed across land use types. Only one species (*G. murinus*) strongly selected the National Park and, to a lesser degree, the pastoral land, but avoided the agricultural land. *A. niloticus* selected the pastoral land most strongly and, to a smaller extent, the National Park, but avoided the agricultural land. Two other species, namely *Aethomys* sp. and *M. natalensis*, strongly selected the pastoral land but weakly selected the National Park and the agricultural land. Lastly, one species, *G. vicinus*, weakly selected the agricultural land, followed by the pastoral land, but avoided the National Park (Fig. 3, Appendices 1 and 2).

Land use selection varied with small mammal species and between the wet and dry seasons (Fig. 4 and Appendix 3). Cumulatively, relative abundance of small mammal did not differ between seasons in the National Park but did so in the pastoral and agricultural lands both of which showed clear seasonal patterns, partially contradicting P_3. Variation in relative abundance across seasons was also observed for individual species such that three species were more abundant in the National Park in the dry than in the wet season (*A. niloticus*, *M. natalensis* and *M. sorella*) whereas *Crocidura* spp., *Mus* sp. and *G. murinus* showed the opposite pattern (Appendices 2 and 3). The relative abundance of two species in the National Park did not vary between seasons (*Aethomys* sp. and *D. melanotis*). By contrast, three species (*Aethomys* sp., *A. niloticus* and *M. natalensis*) were more abundant in the pastoral land in the dry than in the wet season, such that *M. natalensis* and *A. niloticus* were two times more abundant in the dry than in the wet season, supporting P_2 and P_4. Two more species showed similar but weaker selection patterns (*G. vicinus* and *M. sorella*). In addition, *G. vicinus* was the most (6.3 times more) abundant in the dry than the wet season in the agricultural land (Figs. 3 and 4, Appendix 2). The ratios of all the other species between the dry and the wet seasons were at most unity.

The small mammals also selected contrasting habitat types but were distributed over most of the five habitat types. This implies interspecific differences in preferred habitat types. Specifically, six species were trapped in all the five habitat types. Two species were not captured at all in the riverine forest habitat (*M. natalensis* and *G. vicinus*) and one each in the wooded grassland (*G. murinus*) and grassland (*G. vicinus*). The most preferred habitat type varied with species and was the riverine forest for one (*G. murinus*), shrubland for six (*A. niloticus, Crocidura* spp., *D. melanotis, G. vicinus, M. sorella* and *Mus* sp.) and cropland for two *(Aethomys* sp. and *M. natalensis*) species (Appendix 1 and 3). The second most preferred habitat type also varied between species and was wooded grassland for three (*A. niloticus, Crocidura* spp. and *D. melanotis*), shrubland for one (*M. natalensis*) and cropland for two (*Mus* sp. and *G. vicinus*) species (Fig. 3, Appendix 2).

Habitat selection interacted with land use so that the same species selected different habitat types in different land uses. The following examples illustrate this interaction. In the National Park, some species selected wooded grassland, shrubland and riverine forest (*Crocidura* spp.), wooded grassland and shrubland (*D. melanotis*), or almost exclusively, the riverine forest (*G. murinus*) (Appendix 2). Moreover, some species primarily selected cropland in the pastoral land (*Aethomys* sp.) while others selected shrubland in the pastoral land but wooded grassland in the National Park (*A. niloticus*). One species primarily selected cropland in the pastoral land but shrubland in the agricultural land (*G. vicinus*) whereas another strongly selected cropland, in both the pastoral and agricultural lands, and shrubland, in the pastoral land but wooded grassland in the National Park (*M. natalensis*). Finally, one species selected shrubland in the agricultural land but grassland in the National Park (*M. sorella*), while another species mostly selected riverine forest and shrubland in the National Park but cropland in the agricultural and pastoral lands (*Mus* sp.) (Fig. 3).
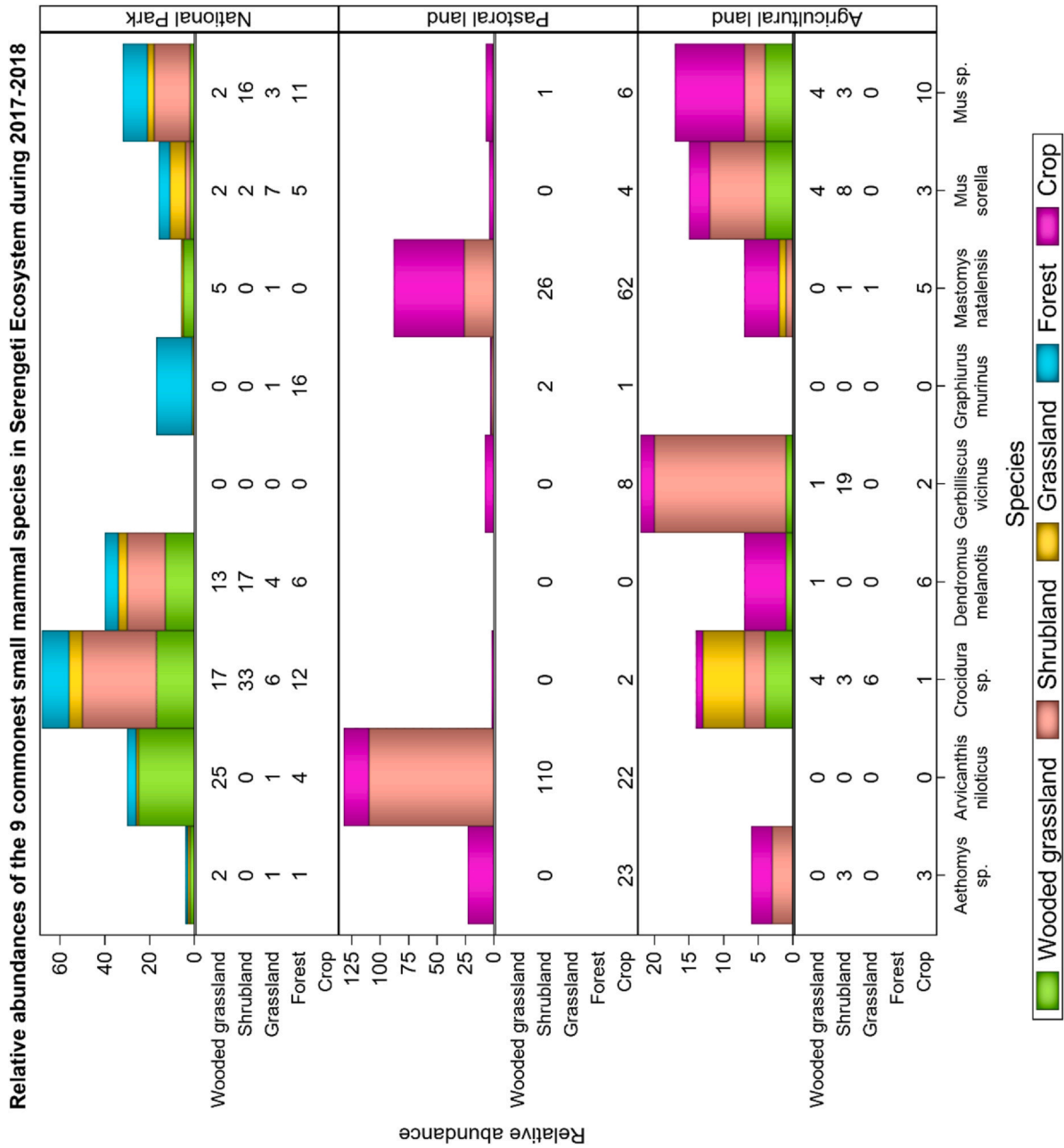
Fig. 3. Relative abundances of the first-time captured individuals of the nine commonest small mammal species trapped during 28,200 trap nights of effort in each of the five habitat types distributed over three land use types in the Serengeti Ecosystem during 2017 and 2018.
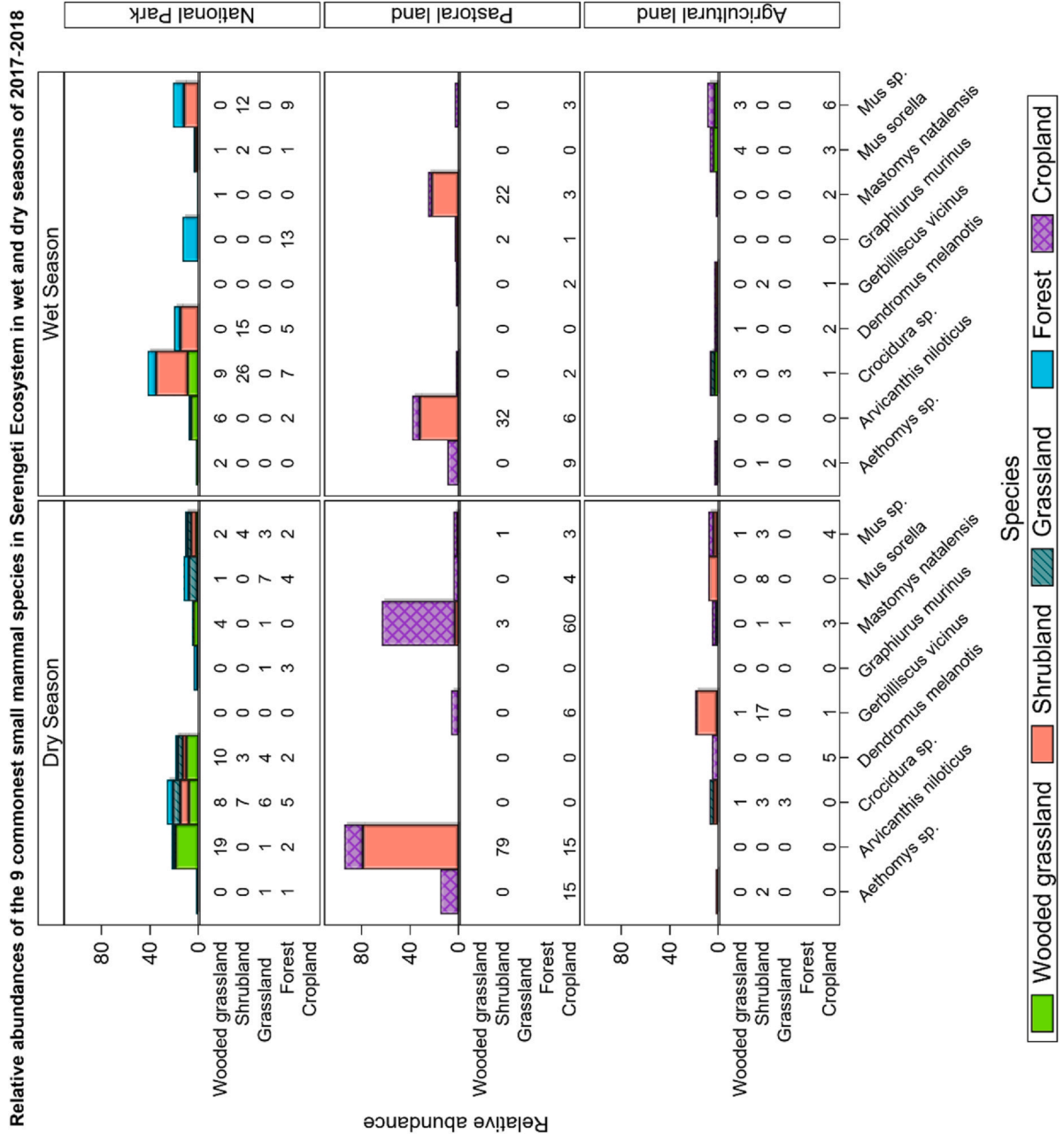
Fig. 4. Relative abundances of the nine commonest small mammal species trapped during 28,200 trap nights of effort in each of the five habitat types distributed across three land use types in the Serengeti Ecosystem during the dry (August and September) and wet (April and May) seasons of 2017 and 2018.

Habitat selection in each land use was generally consistent between seasons for four species (*Aethomys* sp., A. *niloticus*, *Crocidura* spp. and *Mus* sp.) but inconsistent for others (Appendix 3). For *A. niloticus* the stronger selection of the shrubland in both seasons indicates preference for this particular habitat type. In the National Park, *D. melanotis* mainly selected wooded grassland in the dry season but shrubland in the wet season but its relative abundance varied little between seasons in the pastoral and agricultural lands. Furthermore, another species, *G. vicinus,* selected shrubland in the agricultural land but cropland in the pastoral land in the dry season and showed evidence of stronger selection of the shrubland in the agricultural land than in the cropland in the pastoral land. Yet, *Crocidura* spp. selected the grassland in the National Park in the dry but not in the wet season and selected mainly the shrubland in the wet than in the dry season. Moreover, one species, *G. murinus*, selected the riverine forest in the National Park mainly in the wet season. *M. natalensis,* strongly selected cropland in the dry season when crops are harvested but shrubland in the wet season in the pastoral land. For a few species, relative abundance was too low to reliably assess selection in the wet (*G. vicinus* and *Mus sorella*) or dry (*G. murinus*) season. In addition, most of the small mammal species were nocturnal except for *A. niloticus* that was diurnal mostly in the shrubland habitat (Appendix 3).

3.3. Characteristics of used microhabitats

Characteristics of the used microhabitats varied across habitat types, land uses and seasons (Figs. 5 and 6). Notably, grass cover varied more than herb, shrub or tree cover between seasons and was relatively higher in the wet than the dry season in all the three land uses. Grass cover varied little between seasons in the grassland habitat but increased in the wet season in the wooded grassland habitat in the agricultural land. Also, herb cover increased in the wet season, the growing season in the cropland habitat in the agricultural land (Fig. 5).

The small mammals used microhabitats with contrasting characteristics (Fig. 6, S2 Table and Appendix 3). All the nine common species used microhabitats with short to medium grasses but some species used microhabitats with tall grasses such as a median height ≥ 50 cm, (*A. niloticus*, *Crocidura* spp., *D. melanotis*, *Mus* sp. and *Mus sorella*) while others preferred mainly microhabitats with short grasses (*Aethomys* sp., *G. vicinus*, *G. murinus* and *M. natalensis*). Similarly, most of the common species used microhabitats with both tall herbs and shrubs (median height ≥ 50 m) but a few used microhabitats with short herbs and shrubs (*Crocidura* spp.*, Mus sorella, D. melanotis*), tall herbs and short shrubs (*M. natalensis*) or only short herbs (*G. murinus*). Most species used microhabitats with low to dense grass cover (*M. natalensis*, *Crocidura* spp.*, Mus sorella* and *A. niloticus*) and only one species used microhabitats with dense tree cover (median cover ≥ 50%) (*G. murinus*). Additionally, some species preferred dense grass cover but mostly during the wet season (*M. natalensis*). Litter depth was generally low in the ecosystem and no clear use pattern for it emerged.

4. Discussion

Land use and habitat selection varied between species and seasons. Habitat selection interacted with land use, resulting in the same species selecting different habitat types in different land uses. Moreover, the small mammals selected microhabitats with different characteristics. In consequence, the aggregate relative abundance of the small mammals was the highest in the pastoral land, intermediate in the National Park and the lowest in the agricultural land. Nevertheless, relative abundance and its distribution varied among species such that two generalist species, A. *niloticus* and *M. natalensis*, were the most abundant and most widely distributed in the ecosystem. Due to their ability to thrive well in disturbed habitats, these species tolerate a wide range of habitats in the Serengeti Ecosystem (Senzota, 1978, Magige and Senzota, 2006) and elsewhere in Southern Africa (Makundi et al. 2007, Makundi et al. 2010).

The land use and habitat selection patterns are only partially predictable from knowledge of the ecological requirements of the species. This is not surprising because multiple factors shape habitat selection by small mammals at the ecosystem scale. Thus, even though our data and models enabled us to explore and characterize land use, habitat and microhabitat selection by small mammals, we do not expect the models to have high explanatory power because we considered relatively few variables. More, crucially, the relatively few non-zero captures for individual species partly due to short trapping periods, rarity and small home ranges of most of the species likely undermine the power of statistical tests. Together with spatial heterogeneity characteristic of large systems, such as the Serengeti, these features collectively make accurate prediction of habitat selection exceedingly challenging.

Even so, the results illuminate land use and habitat selection patterns and how they vary between small mammal species and seasons. The National Park apparently provides more suitable habitats for the majority of the common small mammal species that therefore selected it (*Crocidura* spp.*, D. melanotis, G. murinus* and *M. sorella* and *Mus* sp.) than either the pastoral or agricultural land, similar to findings of other studies (Taylor et al. 2007, Rautenbach et al. 2014). The strong selection of the National Park indicates preference for specific habitat attributes such as tall vegetation (*G. murinus*) and leaf litter for cover and food (*Mus* sp.) prevalent in the park (Ofori et al. 2015). Habitat and diet generalists able to survive in a wide variety of habitats were widely distributed across habitats, as expected, but were more abundant in some habitat types than others, thus indicating selection. More precisely, three generalist species (*A. niloticus, M. natalensis* and *Aethomys* sp.) selected mostly the pastoral land, and to a lesser extent, the National Park. The much higher relative abundance of *A. niloticus* and *M. natalensis* in the pastoral land than in the National Park indicates wide distribution and the superior ability of habitat generalists to survive in a variety of habitat types (Stenseth et al. 2003, Magige and Senzota, 2006). Not surprisingly, both species rank among the most common and serious crop pests across sub-Saharan Africa (Mwanjabe and Leirs, 1997, Massawe et al. 2011), and are
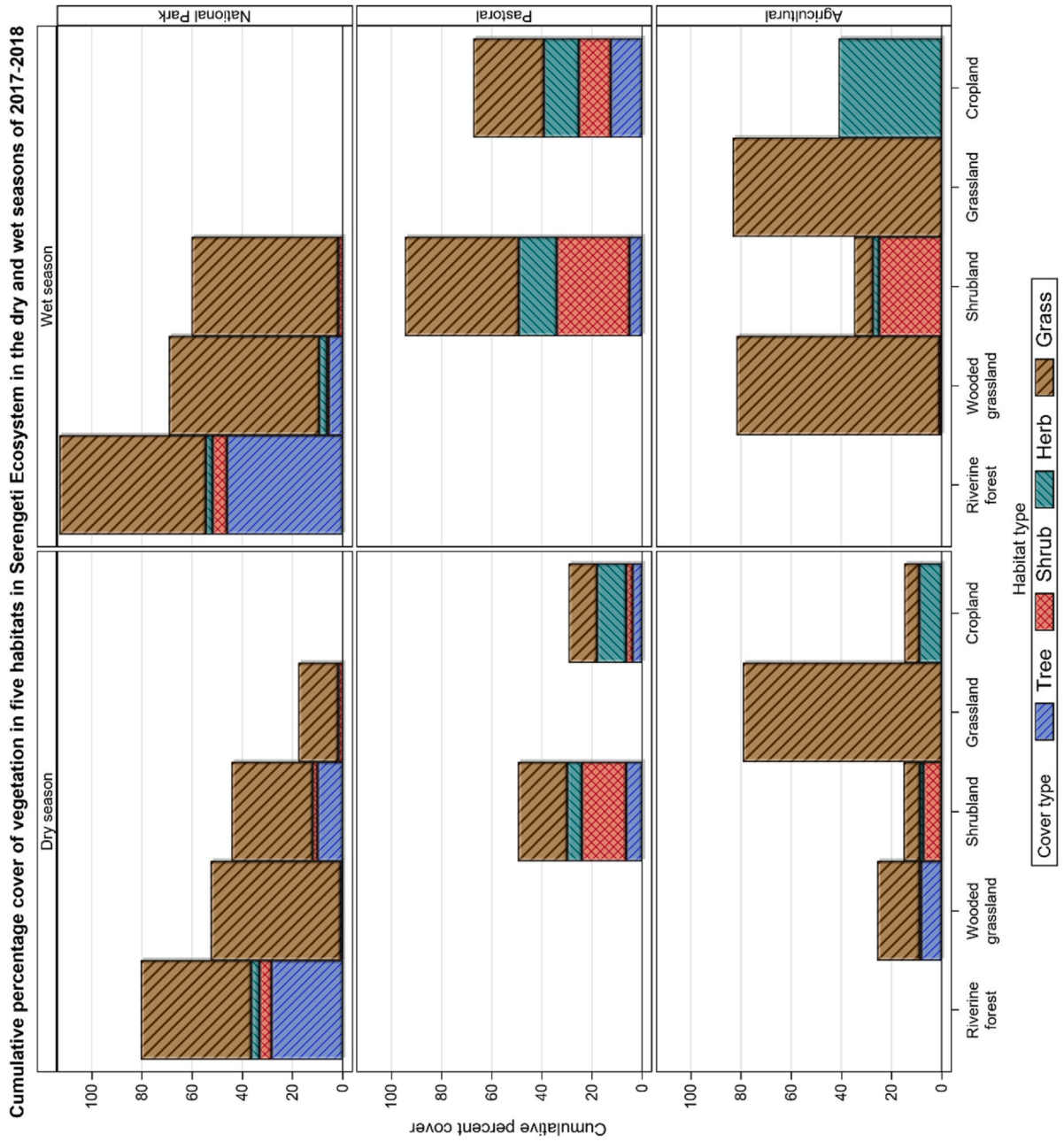
Fig. 5. The cumulative percentage (stacked) cover of trees, shrubs, herbs and grasses in the five habitats located in three land use types in the Serengeti Ecosystem during the dry (August and September) and wet (April and May) seasons of 2017 and 2018.
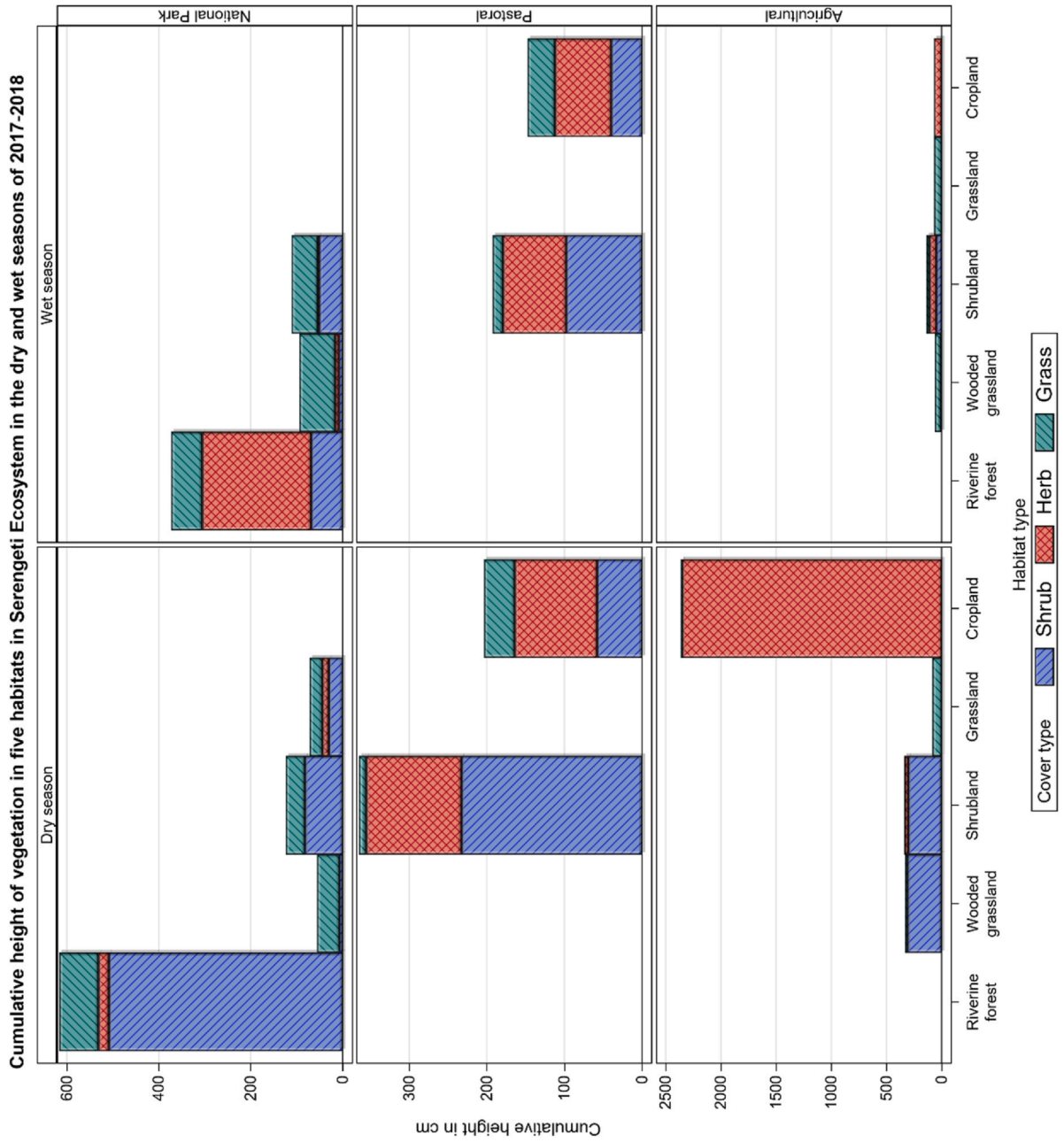
Fig. 6. The cumulative (stacked) height (cm) of shrubs, herbs and grasses in the five habitat types in the Serengeti Ecosystem during the dry (August and September) and wet (April and May) seasons of 2017 and 2018.

therefore favored by human land conversion. Similarly, the wide distribution of *Mus* sp. across the three land uses but higher relative abundance in the shrubland habitat indicates preference. That this species used habitats with medium grass height and cover portrays a strategy of maximizing food acquisition due to its opportunistic feeding style (Stewart et al., 2000). By contrast, habitat or diet specialists can be expected to select fewer habitats, such as the omnivorous *G. vicinus*, which prefers pre-harvest croplands (Mulungu et al. 2011a) and selected mainly the agricultural land. This species primarily lives in agricultural lands but can migrate to other land uses and habitats, including shrublands (Odhiambo et al. 2008).

Furthermore, small mammals showed distinctive habitat selection patterns within each land use and were widely distributed across the five habitat types. The habitat type selected by the small mammal species reflected their particular but contrasting preferences. First, habitat selection portrays preference for less disturbed habitats, tall vegetation for nesting in tree cavities, or habitat specialization, such as for the riverine forest (*Mus* sp*., Crocidura* spp. and *G. murinus*) (Rowe-Rowe and Meester, 1982, Rautenbach et al. 2014, Kingdon, 2015). Other species demonstrated preference for thick and tall vegetation (Rowe-Rowe and Meester, 1982) by selecting predominantly the riverine forest and wooded grassland (*D. melanotis*). Secondly, habitat generalists able to exploit food in contrasting habitat types selected several habitats, as expected, but still displayed some degree of preference. As an instance, two habitat generalists (*Crocidura* spp. and *Mus* sp.) (Kingdon, 2015, Ofori et al. 2015) selected shrubland and cropland (*Mus* sp.) and shrubland and wooded grassland (*Crocidura* spp.). But *Crocidura* spp. tended to avoid cropland because it prefers habitats with well-developed understory vegetation (Torre et al., 2014) and feeds on invertebrates expected to be more abundant in the National Park than cropland (Schekkerman and Beintema, 2007, Kingdon, 2015). Third, habitat selection also reflected both the feeding style and the structural habitat preferences of some species. Thus, *A. niloticus* showed stronger selection of shrubland than cropland but two species (*M. natalensis* and *Aethomys sp*.) showed the opposite pattern. This can be interpreted as mirroring the preference of *A. niloticus* for a diet consisting of a variety of plant parts, mainly leaves and stems, and some seeds, in contrast to *M. natalensis* and *Aethomys sp*., both of which feed mainly on grains or seeds and, occasionally, on leaves (Senzota, 1978, Kingdon, 2015, Magige, 2016). Moreover, whereas *A. niloticus* selected shrubland and wooded grassland, reflecting its preference for shrubs interspersed with medium grassland (Magige and Senzota, 2006, Mulungu et al. 2011b), *M. natalensis* and *Aethomys* sp. preferred areas with some ground cover, such as thorn fences around agricultural fields as refuges while feeding in the nearby cropland (Linzey and Chimimba, 2008).

The selection of the same habitat by multiple species is only possible if they are separated along some niche dimension. Thus, *A. niloticus* and *M. natalensis* selected both shrubland and cropland habitats but at different times so that they did not simultaneously have high relative abundances in the same habitat, suggesting separation along both temporal and microhabitat dimensions. This was further supported by the fact that *A. niloticus* was mostly diurnal while *M. natalensis* was nocturnal indicating that these two species enhance their co-existence by diel separation (Blanchong and Smale, 2000; Flanagan, 2013; Makundi et al., 2010). On the other hand, *G. vicinus* and *M. natalensis* both selected the shrubland and cropland habitats but *G. vicinus* was more abundant in the shrubland whereas *M. natalensis* was more abundant in the cropland, thus enabling spatial separation and coexistence. The co-existence or co-occurrence of *G. vicinus* with *M. natalensis* in the cropland habitat has also been reported for central Tanzania (Mulungu et al. 2011a). Even so, *G. vicinus* shows weaker preference for cropland habitats than *M. natalensis*. Also, the selection of shrubland in the agricultural land by *G. vicinus* suggests that this species visits the crop fields for food but retreats to the nearby shrublands for safety. This is expected given the omnivorous diet of this species, consisting predominantly of plants (Makundi et al. 2010). Alternatively, the higher relative abundance of the species in the shrubland might reflect its ingestion of less seeds than other plant materials (Odhiambo et al. 2008, Mulungu et al. 2011a).

Land use and habitat selection patterns were generally seasonal with some species (*Aethomys* sp., *A. niloticus*, *Crocidura* spp. and *Mus* sp.) consistently selecting the same land use and habitat type across seasons. Consistent selection of the same habitat type across seasons suggests that it is probably preferred by the species. Seasonality in land use or habitat selection can be driven by multiple factors. First, attraction by the greater availability of seeds or grains around the harvesting period (Kingdon, 2015) can lead to greater relative abundance of a species in the cropland habitat in the dry season, such as the greater abundance of *Aethomys* sp. and *A. niloticus* in the cropland in the pastoral land in the dry season. Second, response to seasonal variation in rainfall and hence in food availability and quality and preferred moist habitats (Kingdon, 2015) can lead to higher relative abundance in a habitat, as was the case for *Crocidura* spp. in the shrubland and forest habitats in the National Park in the more humid wet season. Third, seasonal habitat switching or emigration from locally unfavorable conditions to more favorable nearby habitats (Timbuka and Kabigumila, 2006) can cause seasonal avoidance of certain habitats. Possible causes of seasonal emigration include waterlogging in the wet season or seasonally elevated predation risk (Houston, 1972, Sinclair et al. 2015).

Seasonality in the selection patterns of several species suggest seasonal habitat switching. For example, the avoidance of the grassland habitat in the wet season by some of the species (*Crocidura* spp., *D. melanotis* and *Mus sorella*), the shifting of *D. melanotis* from the wooded grassland in the dry season to the shrubland habitat in the National Park in the wet season, and the higher relative abundance of *G. murinus* in the riverine forest in the National Park in the wet than in the dry season, all indicate seasonal migration probably in response o seasonal fluctuations in the availability of preferred food items such as insects and buds in the forest during the wet season (Nowakowski et al., 2006) Similarly, the omnivorous but mainly granivorous *M. natalensis* (Kingdon, 2015), selected the cropland habitat in the pastoral land in the dry season but switched to the shrubland habitat in the wet season, probably in response to seasonal fluctuations in the availability and quality of food and cover. This is likely because cultivated fields are sown with crops in the wet season and offer plentiful food supply in the harvest period in the dry season. In the wet season, the quality of the crop fields reduces because ploughing reduces plant cover and

food availability for breeding (Massawe et al. 2003). The species apparently responds to this decrease by increasing their use of the surrounding habitats, such as shrubland (Hodara et al., 2000). Lastly, seasonality in habitat selection may portray seasonal fluctuations in population size because small mammal numbers typically increase in the dry season as a result of breeding in the wet season (Bantihun and Bekele, 2015; Shilereyo et al., 2020). The higher relative abundance of *G. vicinus* in the shrubland in the agricultural land and cropland, and to a lesser extent in the pastoral land in the dry season than in the wet season, likely arises from reproductive seasonality and juvenile recruitment. Moreover, the stronger preference of the shrubland than the cropland by *G. vicinus* reflects its greater preference for non-grain diet compared to *M. natalensis* (Makundi et al. 2010).

The land use and habitat selection patterns and their seasonality support the prediction (P_1) that most species should select the National Park and its associated habitats (*Crocidura* spp., *D. melanotis*, *G. murinus, Mus sorella* and *Mus* sp.). These species likely perceive the National Park as safer than the pastoral or agricultural land and are better able to satisfy their basic requirements in the park (Rowe-Rowe and Meester, 1982, Rautenbach et al. 2014). Selection of the cropland habitat by the pest species (*Aethomys* sp., *G. vicinus*, *M. natalensis*, *Mus* sp.) also conforms to the prediction (P_2) that pest species should be common in the agricultural habitats. Moreover, the stronger selection of the cropland most especially during the dry season (*M. natalensis*) supports the prediction (P_4) and suggests preference for seeds, similar to findings of other studies elsewhere in Africa (Delany and Monro, 1986, Mulungu et al. 2011a). However, the selection patterns of other species contradict or partly contradict the predictions of (P_1) that most small mammal species select the National Park and the associated habitats (*Aethomys* sp., *A. niloticus*, *G. vicinus* and *M. natalensis*), (P_2) that pest species will be the most common species in the agricultural and pastoral land than in the National Park (*A. niloticus*, *Crocidura* spp., *G. murinus* and *Mus sorella*) or (P_3) that most species select less disturbed habitats in the National Park, especially in the wet season. (*Aethomys* sp., *A. niloticus*, *Crocidura* spp., *G. vicinus*, *G. murinus* and *Mus sorella*). This is because some of the generalist species (*A. niloticus*, *M. natalensis*, *Mus* sp., *Aethomys* sp.) used multiple habitats and land uses, showed little habitat specialization, or were too rare (*G. murinus* and *D. melanotis*) to reliably establish land use or habitat selection patterns and their seasonality.

The contrasting characteristics of selected microhabitats reflect differences in species requirements, with the majority of the habitat generalists (*Aethomys* sp., *G. vicinus*, *M. natalensis*, *Mus* sp.) exhibiting less specific microhabitat utilization except for *A. niloticus* which occurred mostly in microhabitats with tall grass, likely because of food and cover. Also, the utilization of microhabitats with relatively dense grass cover by *M. natalensis* (wooded grassland and shrubland) during the wet season, suggest this species switches from cropland to other habitats when herb cover and grains are reduced in the cropland. However, selection of tall vegetation is consistent with the arboreal lifestyle of *G. murinus* (Rautenbach et al. 2014, Kingdon, 2015) while selection of vegetation with low shrub cover is essential for concealment of *Mus sp*. from predators (Kingdon, 2015).

5. Conclusions

We analysed land use and habitat selection by small mammals, how the selection patterns vary between the wet and dry seasons and characteristics of the used microhabitats in Tanzania's Serengeti Ecosystem. The patterns we uncovered are intricate, reflecting the multifactorial design, complexity of the patterns shown by the nine different species and lack of a simple unifying pattern. Land use and habitat selection and characteristics of used microhabitats varied among small mammal species and between seasons. Nevertheless, the majority of the species selected at least two of the three land uses and several of the five habitat types, indicating flexibility in habitat selection and utilization. Most of the small mammal species (*Crocidura* spp., *D. melanotis*, *G. murinus*, *Mus sorella* and *Mus* sp.) selected the more intact and safer National Park and tended to avoid the disturbed pastoral or agricultural lands. Furthermore, most species selected the wooded grassland, shrubland and riverine forest habitats, likely because they provide greater safety, moist environments and a wide variety of nesting sites and food items. Opportunistic and pest species, such as *Aethomys* sp., *A. niloticus, M. natalensis* and *G. vicinus* primarily selected the pastoral land followed by the agricultural land and tended to avoid the National Park. Seasonality in land use and habitat selection was manifested mainly in the selection of the National Park and its associated habitats by many species (*D. melanotis, G. murinus, Crocidura* spp. and *Mus* sp.) in the wet and dry seasons except for one species (*Mus* sp.), which selected the agricultural land in the dry season. The habitat generalists, consisting mostly of opportunistic and pest species, selected cropland and shrubland habitats in the pastoral and agricultural lands in the dry season when grains are plentiful but some of them selected the shrubland in the wet season (*M. natalensis*) while others (*G. vicinus*) had too few captures to establish selection patterns for the wet season. Both species that selected cropland during the dry season (*Aethomys* sp. and *M. natalensis*) had lower relative abundance in the same habitat during the wet (ploughing) season. These findings emphasize the need for maintaining high habitat heterogeneity in areas bordering protected areas, and that intensification of human activities in ecosystems and their surrounding areas is likely to increase the abundance of pest and opportunistic species but lower overall species abundance and diversity.

Ethics Statement

The study design was approved by the Tanzania Wildlife Research Institute (TAWIRI) and the permit to conduct the research was obtained from the Tanzania Commission of Science and Technology (COSTECH) and Tanzania National Parks (TANAPA). All captured small mammals were handled according to the approved permit and released immediately at the point of capture after observation.

Declaration of Competing Interest

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01606.

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