The small mammal community of Mukogodo Forest, Kenya

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Abstract

Species richness and diversity of rodents and insectivores were investigated at relict forest patches of Mukogodo, Laikipia, Kenya using Sherman's live traps and pitfall traps. Two hundred and nineteen individuals were captured in 3021 trap-nights. There were eleven species in two taxonomic groups, Rodentia and Insectivora. Two other rodent species were sighted but not captured. Thirteen bats belonging to four species (*Epomophorous wahlbergi*, *Pipistrellus kuhlii*, *Scotophilus dingani* and *Nycteris thebaica*) were opportunistically trapped using mist nets. Two of the four species accumulation curves for forest patches did not reach an asymptote. Species richness and diversity were highest at Kurikuri compared with other patches because of habitat variability. The results support the prediction that forest disturbance and degradation lead to an increase in generalist species as compared with specialists and highlight the importance of relict afromontane forests in the conservation of small mammals in Kenya.

Key words: disturbance, Kenya, Mukogodo, small mammals

Résumé

On a étudié la richesse et la diversité des espèces de rongeurs et d'insectivores dans des îlots forestiers résiduels de Mukogodo, Laikipia, au Kenya, en se servant de pièges Sherman et d'autres trappes. On a capturé 219 individus en 3.021 nuits-piège. Il y avait 11 espèces appartenant à deux groupes taxonomiques, les Rodentés et les Insectivores. Deux autres espèces de rodentés ont été aperçues mais pas capturées. 13 chauves-souris appartenant à quatre espèces (*Epomophorous wahlbergi*, *Pipistrellus kuhlii*, *Scotophilus dingani*, et *Nycteris thebaica*) ont été attrapées par hasard dans des filets japonais. Deux des quatre courbes d'accumulation des espèces n'atteignaient pas l'asymptote dans les îlots forestiers. La richesse et la diversité des espèces étaient les plus élevées à Kurikuri en raison de la variabilité de l'habitat. Les résultats soutiennent la prédiction selon laquelle la perturbation et la dégradation de la forêt entraînent une augmentation des espèces généralistes par rapport aux espèces spécialisées et soulignent l'importance des résidus de forêt afromontagnarde pour la conservation des petits mammifères au Kenya.

Introduction

The remnant dry afromontane forests of Mukogodo, Laikipia, Kenya are among the most threatened biomes of Kenya. The forests are essentially 'ecological islands' surrounded by a matrix of human activity and encroachment. The forests are threatened by human population increase, expanding demand for land for pasture, settlement and farming, forest exploitation, and tourism development. These factors pose serious threats to animal communities, while most components of these communities remain largely unknown. Two important threats to Mukogodo forest reserve are fire and grazing pressure. The indirect effects of this grazing pressure and effects of fire as a result of honey gathering on small mammals occurring in the forest have not been studied. Whilst an anecdotal and generalized record of large mammals occurring at Mukogodo forest reserve is available, none is present for small mammals. While information on small mammal ecology in the tropics remains largely scanty (Barnett & Dutton, 1995), in Kenya it contains isolated biotopes such as the savannah (Cheeseman & Delany, 1979; Alibhai & Key, 1985; Schwan,

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1986). This study reports on the first list of rodents and insectivores present at Mukogodo forest reserve with implications to the conservation and sustainable management of the forest. Bats are also presented but not discussed.

Materials and methods

Study area

This study was conducted at Mukogodo forest reserve (0°16′N and 0°32′N; 37°11′E and 37°20′E), Laikipia, Kenya at elevations ranging from 1100 to 2140 m a.s.l. (Fig. 1). Mukogodo forest reserve is classified as a dry afromontane forest dominated by numerous cedar (*Procera juniperus*) and Podocarpus [*Podocarpus falcatus* Mirb. and *P. latifolius* Thunb. (Mirb.)] trees. The reserve is owned by four adjacent Maasai Group Ranches; Kurikuri, Makurian, Illingwesi and Lekurruki with each Group Ranch having a clearly defined area for its jurisdiction. The reserve is a major source of dry season grazing for the local Maasai population. Forest ponds, streams and rivers are an important source of water both for the people and their livestock, especially in the dry season. Honey gathering is a common practice in the forest both as a food source and for making local brews. Anecdotal evidence, however, suggests that honey gathering causes uncontrolled fires within the forest. Additionally, the Maasai rely on the

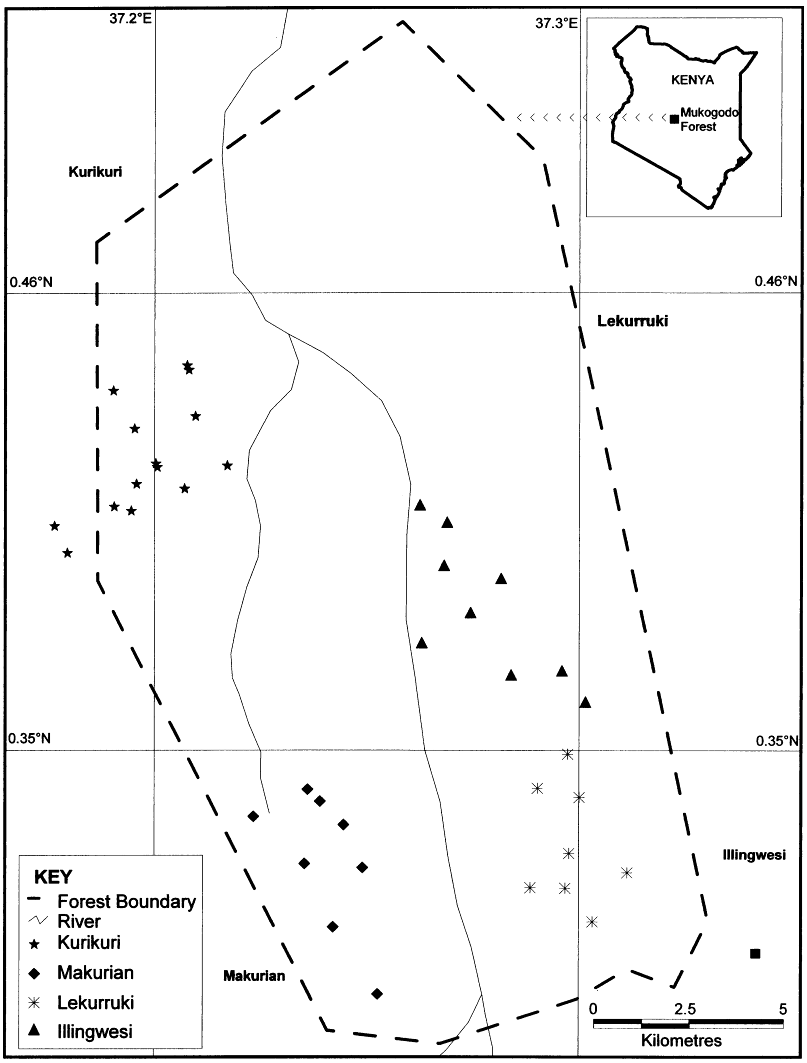

Fig 1 Map of Mukogodo forest showing the location of study sites.

forest for medicinal plants, vegetables, fruits, nuts and tubers. Of major importance is the social and cultural attachment of the local community to the forest. The community has traditionally used the forest for traditional ceremonies and worship and this has led to some form of protection. Because of their cultural importance, the preservation of the remnant forests would maintain traditional values of the local people.

Methods

Trapping carried out in March, June and July of 2004. Small mammals are difficult to survey because, in order to avoid predation, they have evolved dull coloration, secretive behaviour and in many cases nocturnal habits (Delany, 1975). As different species of small mammals are selectively trapped in relation to the type of traps and capture technique (Pucek, 1969), we applied two trapping methods, Sherman's live traps and pitfall traps. Folding Sherman's live traps made of aluminium (230 × 95 × 80 mm, H. B. Sherman's Traps, Inc., Tallahassee, FL, U.S.A.) were used to capture rats and mice while pitfall traps were used for trapping soricids and small mice. All traps were set in the different microhabitats ranging from forest edge, montane grasslands, gallery forest, savannah woodlands, secondary forest and riparian vegetation. Bait for the Sherman's live traps included a mixture of peanut butter with maize meal, fried coconut and mashed ripe bananas to attract a wide array of small mammals. Each transect or trap line consisted of an average of 50 traps that were spaced 5–10 m apart. Traps were inspected daily in the morning. After five consecutive nights of trapping the trap lines were shifted to a different microhabitat. Pitfall traps consist of a drift fence constructed from metal wire mesh (mesh size 5 × 5 mm) approximately 30 cm in height and 20–25 m in length. The fence acts as a barrier to foraging animals, guiding them into sunken 5-l plastic buckets (20 cm in diameter × 25 cm in depth). The pitfalls were distributed in 30–50 m lines and comprised of buckets set every 5 m.

Two types of mist nests were employed to capture bats at ground level: 18 × 2.8 m and 12 × 2.8 m (36 mm mesh) with five shelves. Total sampling effort was 54 net hours for 18 m nets and 52 net hours for 12 m nets.

Small mammals were captured and identified to genus level following the established taxonomic nomenclature (Kingdon, 1971–74, 1997; Meester & Setzer, 1971–77; Delany, 1975; Wilson & Reeder, 1993) and released at the point of capture after marking them by toe clipping. Because it was not possible to identify all of the small mammals in the field, some were prepared and retained as sample specimens. Each specimen was identified where possible to genus level, weighed (to the nearest gram), the state of the vagina or position of the testes noted and the following measurements taken: head and body length, tail, hind foot and ear length (to the nearest millimetre; Nagorsen & Peterson, 1980).

Data analyses

Diversity calculations were performed by programmes given in Krebs' Ecological Methodology (Krebs, 1992). 'Species richness' is the simplest concept of species diversity – the number of species in the community (McIntosh, 1967 in Krebs, 1992). If species richness is only measured on its own, the composition of the community is ignored. For example, the community could be made up of equal numbers of all species, or be dominated by one or two species. Therefore, the evenness of diversity is thus also measured, known as the 'species heterogeneity' (Good, 1953 in Krebs, 1992) or 'species diversity' (Hurlbert, 1971 in Krebs, 1992).

Species diversity for all the sites sampled was computed using the modified inverse of Simpson–Yule diversity of concentration, *C*, for equally abundant species (Dunstan & Fox, 1996):

$$D = 1/(\sum p_i^2)$$

p_i is the proportional abundance of the ith species, given by $p_i{=}n_i/N, i{=}1,2,3\ldots S$. S = species richness which equals to the total number of species in a community. As an index, S is easily conceptualized and comparable across habitats. N = total number of individuals.

The Simpson's index was preferred in this study because it is weighted more towards the abundance of the common species (emphasizes evenness) rather than providing a measure of species richness. Evenness values were derived from the Shannon–Weiner (H') index of diversity. Evenness values were derived from the expression, $E_1 = H'/ \ln S$, where ln S is the natural logarithm of the number of species. Evenness values indicate how the species are distributed in a community. When the evenness is high, the mammal fauna is diverse and the species are equally abundant (Magurran, 1988).

In order to standardize data for all sites sampled so that productivity of habitats were compared, despite the differing trap effort, trap success (the number of animals per 100 trap nights) was calculated from the expression:

$$\text{Trap success} = \frac{\text{Total catch}}{\text{Trap nights}} \times 100$$

Trap success refers to the number of animals trapped per 100 trap nights. It gives an indication of the productivity of the communities sampled in that the higher the trap success the higher the productivity of a given habitat.

Using daily trapping records, species accumulation rates were examined at the end of a sampling regime to estimate the extent to which further trapping would add to the species list and facilitate comparisons of species richness between habitats for any given level of sampling effort.

All small mammals currently known in Kenya were classified according to habitat requirements. The following ecological type categories were recognized for this study as adopted from Kasangaki, Kityo & Kerbis (2003):

1 Forest dependent species (F-species) are largely confined to closed canopy forest and would be unlikely to tolerate any form of large-scale habitat modification although they may persist in secondary forest and isolated forest fragments.

2 Forest nondependent species (f-species) are not restricted to closed canopy and may occur in forest edge, gallery forest and dense savannah woodland.

3 Nonforest (open) habitat species are characteristic of open grasslands and semi-arid environment (O), Aquatic or swamp habitat (A) or occur in a wide range of habitat (W).

4 Where the species ecological category is not defined (U) has been used.

Results

Species richness

A total of 219 small mammals belonging to orders Rodentia (n = 214) and Insectivora (n = 5) were trapped (Tables 1 and 2) out of a total of 3021 trap-nights.

High species diversity and richness of rodents and shrews was recorded at Kurikuri Group Ranch compared with other sites (Table 1). Trap success was equally highest at Kurikuri and lowest at Makurian. However, although Kurikuri recorded the highest diversity and species richness, evenness values were highest at Makurian.

Species accumulation rates showing an increase in the number of species with an increase in the number of

Table 1 Record of species richness, trap nights, trap success, Simpson's diversity (D) index and Shannon's evenness (E_1) at different sites of Mukogodo Forest, Kenya in 2004

	Number of individuals captured by site				
Species	Kurikuri	Makurian	Lekurruki	Illingwesi	Total
Aethomys hindei (Thomas 1902)	38	5	18	12	73
Lemniscomys striatus (Linnaeus 1758)	30	3	7	0	40
Graphiurus murinus (Desmarest 1822)	14	5	1	2	22
Crocidura hildegardeae (Thomas 1904)	2	0	0	1	3
Crocidura jacksoni (Thomas 1904)	0	0	2	0	2
Paraxerus ochraceus	13	4	2	7	26
Acomys wilsoni (Thomas 1892)	1	0	0	0	1
Grammomys dolichurus (Smuts 1832)	36	8	2	1	47
Mus minutoides (Smith 1834)	0	0	0	3	3
Myomys fumatus (Peter 1878)	0	0	0	1	1
Mastomys natalensis (Smith 1834)	0	0	1	0	1
Total (individuals)	134	25	33	27	219
Observed species richness	7	5	7	7	11
D	4.48	4.49	2.82	3.49	
E_1	0.826	0.966	0.710	0.798	
Trap nights	1053	819	516	633	3021
Trap success (%)	12.73	3.05	6.40	4.27	7.25

Table 2 List of small mammal captures from Mukogodo Forest, Lakipia, Kenya in 2004

Order	Family	Species	Number of individuals	Habitat type
Rodentia	Muridae	*Aethomys hindei*	73	O
		Lemniscomys striatus	40	O
		Mastomys natalensis	1	W
		Acomys wilsoni	1	O
		Grammomys dolichurus	47	W
		Mus minutoides	3	W
		Myomys fumatus	1	W
	Scuiridae	*Xerus rutilus*	12[a]	O
		Paraxerus ochraceus	26	f
	Myoxidae	*Graphiurus murinus*	22	W
	Hystricidae	*Hystrix cristata*	10[b]	W
Insectivora	Soricidae	*Crocidura hildegardeae*	3	U
	Soricidae	*Crocidura jacksoni*	2	f
Chiroptera	Pteropodidae	*Epomophorus wahlbergi* (Sundevall, 1846)	8	W
	Vespertilionidae	*Pipistrellus kuhlii* (Natterer, 1817)	2	W
	Vespertilionidae	*Scotophilus dingani* (A. Smith, 1833)	1	W
	Nycteridae	*Nycteris thebaica* (E. Geoffrey, 1818)	2	W

Habitat type or ecological category refers to the general habitat where a species is most likely to be found.
[a]Directly observed.
[b]Counted number of quills in different sites.

captures of rodents and insectivores for each of the sampled sites, i.e. Kurikuri, Makurian, Lekurruki and Illingwesi, behaved differently for each site (Figs 2 and 3). The plots for Kurikuri and Lekurruki reached an asymptote while the reverse is true for Makurian and Illingwesi, illustrating that the inventory of the small mammal community of the relict forests of Mukogodo is far from being complete. Two additional rodent species were observed through either direct observation or through signs. These were the crested porcupine (*Hystrix cristata*, Linnaeus 1758) and the unstriped ground squirrel (*Xerus rutilus*, Cretzschmar 1828). Pitfalls together with drift fences did not yield any insectivores while the Macroscelidea (elephant shrews) were not surveyed at all.

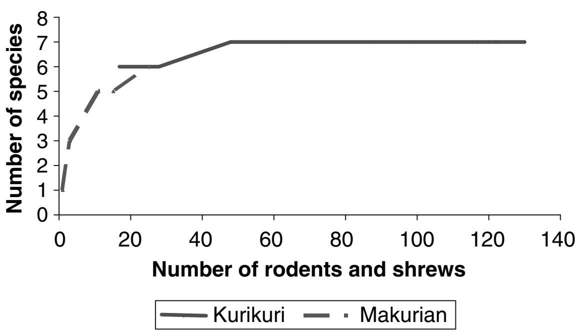

Fig 2 Species accumulation rate for small mammals at Kurikuri and Makurian group ranches from Mukogodo forest, Laikipia, Kenya in 2004.

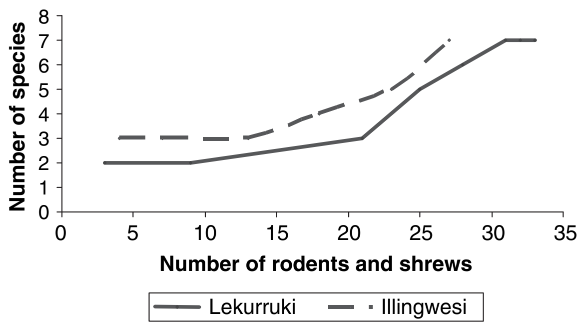

Fig 3 Species accumulation rate for small mammals at Lelurruki and Illingwesi group ranches from Mukogodo forest, Laikipia, Kenya in 2004.

In total, thirteen bats comprising four species, four genera, and three families were captured opportunistically (Table 2). Overall capture success therefore was a lowly 0.12 bats per mist net hour reflecting the little effort put in the sampling of bats.

The small mammal community at Mukogodo largely comprised of species that are either nonforest (open) species i.e. savannah or occur in a wide range of habitats (82.4%; Table 2). Species primarily associated with forest habitat were absent with only two species, *Crocidura jacksoni* (Thomas 1904) and *Paraxerus ochraceus* (Smith 1834), representing forest nondependent species that are not restricted to closed canopy and may occur in forest edge, gallery forest and dense savannah woodland.

Discussion

Thirteen species of rodents and shrews were confirmed to occur at Mukogodo relict forests, the first record of small mammals occurring there. Some of the factors accounting for the relatively low diversity of rodents and shrews could be the increased encroachment of the Maasai herders on the forest through grazing and incidences of fire as well as the relative isolation of the forests from each other and from other nearby remnant forests.

Kurikuri remnant forest recorded the highest species diversity and richness, trap success and number of individual rodents and shrews, but a slightly lower evenness than at Makurian. Higher species diversity at Kurikuri could be attributed to a wide array of vegetation communities ranging from secondary forest to grasslands, woodlands and riparian vegetation. Vegetation at Makurian Group Ranch was largely secondary forest with less ground cover and grasslands that were heavily overgrazed. This means that the forests that appeared to have more understorey cover and with diverse microhabitats were more productive compared with other habitats. In a similar study carried out at Kibale forest in Uganda, Isabirye Basuta & Kasenene (1987) found that the dense understorey of degraded forest had more food resources for rodents and shrews and presented more protective cover and nest sites than the relatively sparse understorey of mature forest. Traditionally the local Maasai use Mukogodo forests as dry-season grazing ground but owing to the burgeoning human population and increasing livestock herds and frequent droughts in the area, the forest is increasingly being degraded especially during the dry season as enormous numbers of livestock are driven into the forest in search of scarce grass, browse and water. Therefore, livestock grazing that is often accompanied by incidences of fire could be major limiting factors on the species diversity of small mammals in these habitats by reducing the understorey vegetation. In a study carried out in the Maasai Mara National Reserve, Kenya, it was found that the combined effect of fire and grazing pressure maintain the wild rodent populations at low densities (Salvatori *et al.*, 2001). In the Mukogodo area, the local Maasai herders use fire to control ticks, reduce cover for predators and to increase palatability of grasses outside the reserve. More often, these fires get out of control and as there is no clear boundary between the reserve and adjacent Group Ranches, the fires may destroy vast sections of the forests. This, combined with grazing pressure, has resulted in a reduction in the ground cover in some sections of the reserve. The extent of favourable habitat in the reserve is, therefore, reduced overall by these two factors and the almost constant presence of either of them may not allow sufficient time for rodent and insectivore populations to reach viable levels.

Some species such as *Mus minutoides*, *Myomys fumatus* and *Acomys wilsoni* were recorded once or twice, suggesting that they are rare. The species appear to be rare because they are sampled in 'marginal' habitats as opposed to their optimal habitats (Basset *et al.*, 1991). Habitat fragments, such as the relict forests of Mukogodo, probably represent 'marginal habitats', hence the high number of singletons in the study. However, species accumulation rates behaved differently for each site (Figs 2 and 3). The plots for Kurikuri and Lekurruki did not only reach an asymptote but levelled off while no asymptotic plateaux were discernible at both Makurian and Illingwesi, which indicates that rodent and insectivore species so far recorded may under-represent species present in these areas. This may be an artefact of the temporal factors associated with this study such as sampling bias but may also indicate relative levels of disturbances among vegetation communities and/or sites of the forest reserve. Therefore increased sampling effort would be expected to yield additional small mammal species in these areas. Reports of reduced species richness of different organisms in forest fragments are well documented (e.g. Pimm, 1998) and larger areas are required to preserve the entire local terrestrial small mammal fauna. The Mukogodo remnant forests are much smaller and would not be expected to preserve the entire small mammal fauna. However, the insectivores are completely under-represented in all sites because pitfall traps did not yield any results and the soricids that are presented here were captured in the Sherman's traps. Additional small mammal species that were recorded through direct observation and/or signs attest to this fact, underscoring the importance of using a variety of different methods to accurately estimate the composition of mammal communities (Pucek, 1969; O'Farrell *et al.*, 1994; Wilson *et al.*, 1996).

All the rodent species recorded in this study are generalist nonforest dependent species suggesting that nonforest conditions may exist in these forests. All sampled relict forests also contained species normally associated with disturbance. Generalist species may be more prevalent in modified habitats as they usually are more common and are less likely to be affected by habitat disturbance or are more likely to re-colonize after a disturbance (Connell, 1978; Denslow, 1985; Hansson, 1991). Less disturbed habitats may favour more specialized species. On the overall, the level of forest degradation at the Mukogodo relict forests is on the increase leading to a skewed community composition in favour of one largely dominant generalist species, the Bush rat *Aethomys hindei*. The loss of forest integrity through loss of understorey cover invariably leads to an increase in rodent species diversity, but at the expense of the original forest-adapted species, as previously suggested by Delany (1986) and Fitzgibbon, Leirs & Verheyen (1995). For more specialized organisms, small mammals or otherwise, the loss of biological diversity in the sites that were sampled is likely to be more severe. Despite their relatively small sizes, the relict dry afromontane forests of Mukogodo, however, still maintain viable populations of nonforest species of small mammals. The results highlight the importance of relict afromontane forests in the conservation of small mammals in Kenya.

While the results of this study may be considered preliminary, they make possible a general interpretation of the condition and integrity of Mukogodo relict forests. Therefore, specific management initiatives such as fire burning to allow regeneration of grasses and herbs for livestock may have deleterious effects on elements of biodiversity. In addition, the grazing of livestock deep inside the forests at Mukogodo may be having serious ecological impacts on resident biodiversity and should be discouraged.

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References

Alibhai, S.K. & Key, G. (1985) A preliminary investigation of small mammal biology in the Kora National Reserve, Kenya. *J. Trop. Ecol.* **1,** 321–327.

Barnett, A. & Dutton, J. (1995) *Expedition Field Techniques: Small Mammals (Excluding Bats)*. Expedition Advisory Centre, London, 125 pp.

Basset, Y., Novotyn, V., Miller, S. & Springate, N.D. (1991) Assessing the impact of forest disturbance on tropical invertebrates: some comments. *J. Appl. Ecol.* **35,** 1–6.

Cheeseman, C.L. & Delany, M.J. (1979) The population dynamics of small rodents in a tropical African grassland. *J. Zool.* **188,** 451–475.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* **199,** 1302–1310.

Delany, M.J. (1975) *The Rodents of Uganda*. British Natural History Museum, London.

Delany, M.J. (1986) Ecology of small rodents of Africa. *Mammal rev.* **16,** 1–41.

Denslow, J.S. (1985) Disturbance-mediated coexistence of species. In: *The Ecology of Natural Disturbance and Patch Dynamics* (Eds S. T. A. Pickett and P. S. White). Academic Press, Tallahasse, Florida, U.S.A. pp. 307–323.

Dunstan, C.E. & Fox, B.J. (1996) The effects of fragmentation and disturbance of rainforests on ground dwelling small mammals on the Robertson Plateau, New South Wales, Australia. *J. Biogeogr.* **23,** 187–201.

Fitzgibbon, C.D., Leirs, H. & Verheyen, W. (1995) Distribution, population dynamics, habitat use of the less pouched rat *Beamys hindei*. *J. Zool.* **236,** 499–512.

Hansson, L. (1991) Dispersal and connectivity in metapopulations. *Biol. J. Linn. Soc.* **42,** 89–103.

Isabirye Basuta, G.M. & Kasenene, J.M. (1987) Small rodent populations in selectively felled and mature forest tracts of Kibale Forest, Uganda. *Biotropica* **19,** 260–266.

Kasangaki, A., Kityo, R. & Kerbis, J. (2003) Diversity of rodents and shrews along an elevational gradient in Bwindi Impenetrable National Park, south-western Uganda. *Afr. J. Ecol.* **41,** 115–123.

Kingdon, J. (1971–74) *East African Mammals: An Atlas of Evolution*, Vols. I, II and IIIB. Academic Press, London.

Kingdon, J. (1997) *The Kingdon Field Guide to African Mammals*. Harcourt Brace and Company, New York, London, Toronto. pp. 364.

Krebs, C.J. (1992) *Ecological Methodology*. Harper & Row, New York, pp. 329–370.

Magurran, A.E. (1988) *Ecological Diversity and Its Measurement*. Croom-Helm, Sydney.

Meester, A. J. & Setzer, A. W. (Eds) (1971–77) *The Mammals of Africa: An Identification Manual*. Smithsonian Institute, Washington DC, U.S.A.

Nagorsen, D.W. & Peterson, L.R. (1980) *Mammal Collector's Manual. A Guide for Collecting, Documenting and Preparing Mammal Specimens for Scientific Research*. Life Sciences Miscellaneous Publications, Royal Ontario Museum, Toronto. pp. 79.

O'Farrell, M.J., Clark, W.A., Emmerson, F.H., Juarez, F.M., Fay, F.R., O'Farrell, T.M. & Goodlett, T.Y. (1994) Use of a mesh live trap for small mammals: are results from Sherman's traps deceptive? *J. Mammal.* **75,** 692–699.

Pimm, S.L. (1998) The forest fragment. *Nature.* **393,** 23–24.

Pucek, Z. (1969) Trap response and estimation of numbers of shrews in removal catches. *Acta Theriol.* **14,** 403–426.

Salvatori, V., Egunyu, F., Skidmore, A.K., De Leeuw, J. & Van Gils, H.A.M. (2001) The effects of fire and grazing pressure on vegetation cover and small mammal populations in the Maasai Mara National Reserve. *Afr. J. Ecol.* **39,** 200–204.

Schwan, T.G. (1986) Comparison of catches of two sizes of Sherman's live traps in a grassland in Lake National Park, Kenya. *Afr. J. Ecol.* **24,** 31–35.

Wilson, D.E. & Reeder, D.M. (1993) *Mammal Species of the World. A Taxonomic and Geographic Reference*, 2nd edn. Smithsonian Institution Press, in association with American Society of Mammalogists, Washington and London.

Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R. & Foster, M.S. (1996) *Measuring and Monitoring Biological Diversity. Standard Methods for Mammals*. Smithsonian Institution Press, Washington.

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