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Chapter 4

Small Mammal Inventories in the East and West Usambara Mountains, Tanzania. 4. Rodentia

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Abstract

During three field seasons between 1991 and 1993, we carried out rodent inventories of the East and West Usambara Mountains, Tanzania. The general trapping protocol used involved both pitfall lines and trap lines (Sherman, Victor, and Museum Special traps), with a limited number of animals trapped within and outside of forest habitats by local people. A total of 885 individual rodents, representing 15 species, were collected during this study. For the East and West Usambara Mountains, 13 (12 native) and 12 (all native) rodent species were recorded, respectively. Most rodents were captured by trap lines (96.6%); a few individuals were captured in the pitfall devices or brought to us by local people. The major exception is that all individuals of *Dendromus* (n = 11) obtained during the survey were in pitfall buckets.

A total of 18,563 sample-nights were accrued over the three years, including 11,339 sample-nights (3314 pitfall-nights and 8025 trap-nights) in the East Usambara and 7224 sample-nights (1924 pitfall-nights and 5300 trap-nights) in the West Usambara Mountains. Based on species accumulation curves, no previously unrecorded species was trapped after 11,064 sample-nights in the East Usambara and after 5213 sample-nights in the West Usambara. However, a previously untrapped rodent (*Graphiurus kelleni*) was captured in the East Usambara on the third-to-last of 59 sampling days, suggesting that other non-canopy-restricted rodent species may have been missed during this survey. In a series of species accounts, information regarding the natural history of the different taxa handled during these surveys, including distribution, ecology, and condition of sexual organs, a list of referable specimens, and the trap devices that collected them, are presented.

Trap and bucket lines combine to effectively sample most small- to medium-sized rodents. However, larger scansorial and canopy-restricted (squirrel) and fossorial (mole rat) species were not captured with our trapping methods, and these tabulations should not be considered a complete list of the small mammals of the Usambaras.

Introduction

The montane forests of Tanzania contain diverse faunal assemblages, many of which have high levels of endemism. Some vertebrate taxa in these forests, such as amphibians, birds, and reptiles, have been studied by multiple generations of field researchers (e.g., Barbour & Loveridge, 1928; Loveridge, 1935, 1937; Moreau, 1935; Stuart, 1983; Newmark, 1991, 2002, 2006; Gravlund, 2002; Bowie et al., 2004; Menegon et al., 2008; Blackburn & Measey, 2009; Newmark et al., 2010). However, mammals, specifically the smaller species, have received notably less attention. Although there have been previous investigations of Tanzanian montane forest shrews (Hutterer, 1986; Stanley & Olson, 2005), bats (Kock & Howell, 1988; Kock et al., 2000), and rodents (Makundi et al., 2003, 2006; Carleton & Stanley, 2005), the past two decades have seen first-time small mammal surveys on mountains across the country (e.g., Stanley et al., 1996, 1998a, 2007a,b; Stanley & Hutterer, 2007; Mulungu et al., 2008). Over the course of three field seasons between 1991 and 1993, we carried out field inventories of the small mammals of the East and West Usambara Mountains, which are part of

the Eastern Arc Mountains. Here, we present the results of these rodent surveys, whereas those pertaining to shrews and bats are reported in Stanley et al. (this volume a) and Stanley and Goodman (this volume), respectively.

Several different studies have been conducted on the rodents of Tanzania in lowland areas associated with their role in diseases that affect humans or as crop pests (e.g., Leirs et al., 1997; Mwanjabe & Leirs, 1997; Makundi et al., 2008). The importance of commensal rodents and their ectoparasites as reservoirs of plague has generated considerable research in montane areas, particularly in the West Usambara Mountains (e.g., Makundi, 1995; Kilonzo et al., 1997).

Based on preliminary inventories, Rodgers and Homewood (1982) listed known mammal species, including rodents, from the East and West Usambara Mountains. Subsequently, through a series of field inventories on different massifs, there has been a focus on the rodent faunas of relatively intact montane habitats across the Eastern Arc Mountains (Stanley et al., 1998a,b, 2007a,b; Stanley & Hutterer, 2007), based on surveys of up to two months. The current study compiles data on East and West Usambara rodents living in several different natural and anthropogenic habitats, including monotypic

TABLE 1. Rodent species and number of individuals captured in traps or pitfall lines in three seasons of faunal surveys of the East and West Usambara Mountains between 1991 and 1993 based on accrued sample nights.

Mountain range	East Usambara				West Usambara				Totals
	1991	1992	1993	EU Total	1991	1992	1993	WU Total	
Accrued number of sample nights	476	8252	2611	11,339	5213	1512	499	7224	18,563
Species									
<i>Dendromus mystacalis</i>	0	11	0	11	0	0	0	0	11
<i>Beamys hindei</i>	0	6	2	8	1	0	0	1	9
<i>Lophuromys aquilus</i>	8	91	19	118	42	8	2	52	170
<i>Aethomys hindei</i>	0	0	0	0	1	0	0	1	1
<i>Grammomys ibeanus</i>	0	3	0	3	19	1	2	22	25
<i>Grammomys macmillani</i>	0	10	1	11	11	0	0	11	22
<i>Hylomyscus arcimontensis</i>	5	31	9	45	93	43	5	141	186
<i>Mastomys natalensis</i>	0	1	0	1	7	0	0	7	8
<i>Mus minutoides</i>	0	1	0	1	1	0	0	1	2
<i>Praomys delectorum</i>	6	186	54	246	80	66	18	164	410
<i>Rattus rattus</i> ¹	0	4	0	4	0	0	0	0	4
<i>Graphiurus kelleni</i>	0	0	1	1	0	0	0	0	1
<i>Graphiurus murinus</i>	0	4	0	4	15	3	0	18	22
Total no. of individuals	19	348	86	453	270	121	27	418	871
Total no. of species	3	10	6	12	10	5	4	10	13
Trap success for rodents (%)	4.0	4.2	3.3	4.0	5.2	8.0	5.4	5.8	4.7

¹ Non-native species.

plantations of tea (*Camellia sinensis*) and *Eucalyptus*, fallow and recently tilled agricultural land, and native montane forest.

Study Area

Stanley et al. (this volume b) detail the specific study sites and the dates of the field inventories. Rodents were sampled from forested and agricultural sites on the Bulwa, Kwamkoro, and Monga Tea estates in the East Usambara and the Ambangulu Tea Estate in the West Usambara between 1991 and 1993 (see Stanley et al., 2011b, figs. 3–5).

Materials and Methods

The general trapping protocol used during this study involved both pitfall lines and trap lines; Stanley et al. (this volume b) report the specific details on these techniques. Although some rodents were captured in pitfall buckets, these were relatively limited and tended to be small species or juveniles of larger taxa. Given that each trap was checked in the early morning and again in the mid-afternoon (while adding fresh bait), the period that an animal was captured, hence activity period, could be ascertained as to between dusk and dawn or between dawn and dusk. A “bucket-night” or “trap-night” refers to one bucket or one trap in operation for a 24-h period (0700–0700 h), and the term “sample-night” is used in discussion of overall sampling effort (the combined number of bucket-nights and trap-nights). In a few cases, people living in vicinity of the study sites trapped various rodents within and outside of forest habitats and offered these animals to us.

We follow the species definitions of Holden (2005) for the Gliridae, Musser and Carleton (2005) for the Muridae and Nesomyidae, Thorington and Hoffman (2005) for the

Sciuridae, and Woods and Kilpatrick (2005) for the Bathyergidae. Field Museum of Natural History (FMNH) catalog numbers are presented for cited vouchers in each species account. Details are also given on the trapping method for each captured animal; specific placement of the pitfall lines (PF) and trap lines (TRL) are presented in Stanley et al. (this volume b).

External measurements accurate to 1 mm were recorded for each specimen by one of the two field collectors (S.M.G. and W.T.S.), and definitions of these measures and their acronyms are presented in Stanley et al. (this volume a). Adult rodents are defined as having a fully erupted third upper molar and completely fused suture between the basioccipital and basisphenoid bones. When describing aspects of the reproductive state of males, testes are described as either abdominal or scrotal and measurements are presented in millimeters as length by width. The epididymis is referred to as either convoluted or not convoluted.

Results

A total of 1311 mammal specimens was collected during this three-year study, including 885 individual rodents representing 15 species. For the East and West Usambara Mountains, 13 (12 native) and 12 (all native) rodent species were recorded, respectively. Most captured rodents (96.6%) were from the trap lines; a few were captured in the pitfall devices (notably, all individuals of *Dendromus* [n = 11] obtained during the survey) or brought to us by local people. A total of 17,692 sample-nights were accrued over the three years, including 11,081 sample-nights (3314 pitfall-nights and 7767 trap-nights) in the East Usambara and 6611 sample-nights (1936 pitfall-nights and 4675 trap-nights) in the West Usambara (Table 1).

In the context of our trap and pitfall efforts (excluding specimens caught by hand), 1132 specimens were collected,

representing 13 rodent species. The East Usambara yielded 12 species of rodent and the West Usambara 10 species of rodent. As demonstrated previously for montane areas of east Africa (Stanley et al., 1996, 1998a,b), trap and bucket lines combine to sample the shrew and small- to medium-sized rodent faunas of a given area effectively.

Stanley et al. (this volume b) presents species accumulation curves separately across the three-year study (1991–1993) for the East and West Usambaras. No previously unrecorded species was trapped after 10,804 sample-nights in the East Usambara (where sample-nights totaled 11,081) and after 4600 sample-nights in the West Usambara (where sample-nights totaled 6611). The final previously untrapped rodent species obtained in the East Usambara was *Graphiurus kelleni*, which was captured on the third-to-last of 59 sampling days, suggesting that other non-canopy-restricted rodent species may have been missed during this survey.

Accounts of Species

Fifteen rodent species were documented for the East and West Usambara Mountains combined during the three-year study. External measurements are presented in Tables 2 and 3. In the following accounts, information for each species regarding their natural history (including distribution, ecology and reproduction), specimens examined (including museum catalog numbers and identifying pitfall lines [PF] and trap lines [TRL] where each specimen was collected [see Stanley et al., this volume b]), and, when necessary, other remarks are presented.

Family Sciuridae

Paraxerus vexillarius (Kershaw, 1923)

DISTRIBUTION—The type locality of *Paraxerus vexillarius* is Lushoto, West Usambara (Kershaw, 1923). Kingdon (1974a, 1997) states that this species is only known from this massif. However, specimens referable to *P. vexillarius* have been collected in the Nguru, Rubeho, Udzungwa, Ukinga, and Uluguru Mountains (in FMNH). The Usambara specimens exhibit the orange feet and tail tip characteristic of the species (Kingdon, 1974a).

ECOLOGY AND REPRODUCTION—Three female *P. vexillarius* were captured by hunters using dogs and brought to our camp on 21 July 1991. The reproductive tracts of two specimens were examined: One was nulliparous and the other had one placental scar in the left uterine horn. External measurements are presented in Table 2.

SPECIMENS EXAMINED—**WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (captured by hand—FMNH 147236, 147237, 147403).

Family Nesomyidae: Subfamily Dendromurinae

Dendromus mystacalis (Heuglin, 1863)

DISTRIBUTION—This species is distributed across central and eastern Africa, from southern Sudan to Angola and eastern South Africa (Musser & Carleton, 2005). Within Tanzania, specimens have been collected in various habitats, including dry woodland areas (e.g., Tarangire National Park [Stanley et al., 2007c]), and zones of higher elevation from western Tanzania, such as the Mahale Mountains (W. T. Stanley, unpubl. data) to the East Usambara.

ECOLOGY AND REPRODUCTION—We trapped eight males and three females in 1992 but none in 1991 or 1993. The testes positions in five males were scrotal and in the other three abdominal. The mean testis measurement in six dissected specimens was 5.3 by 3.2 mm, and all but one individual had convoluted epididymides. Of the two females examined, one had large teats and the other small.

All *Dendromus* were captured by pitfall lines installed in tea plantations. Pitfall line 16 was the most productive for this species, especially near the middle of the line, catching nine of the 11 individuals (82%) collected. *Dendromus* was the most common mammal we captured in tea plantation habitat. External measurements are presented in Table 2.

COMMENTS—Musser and Carleton (2005) suggest that this species as currently configured may contain more than one species. The holotype was collected in Ethiopia, a considerable distance from the Eastern Arc Mountains. Specimens collected during this study were identified by the fifth hind toe having a claw (as opposed to a nail) and greatest length of the skull less than 22 mm (Misonne, 1974).

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, control site (PF 29—FMNH 150098); 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 150092–150097, 150424–150426; PF 24—FMNH 150427).

Family Nesomyidae: Subfamily Cricetomyinae

Beamys hindei (Thomas, 1909)

DISTRIBUTION—The genus *Beamys* is known to occur from southeastern Kenya to the eastern half of Tanzania and south into Malawi and Zambia (Musser & Carleton, 2005). Within Tanzania, *B. hindei*, as currently defined, has been recorded in lowland coastal forests and montane areas (Christensen, 1987; Fitzgibbon et al., 1995; Stanley et al., 1998a,b). We have recorded it in the following montane areas within Tanzania (north to south): South Pare, West Usambara, East Usambara, Ukaguru, Nguu, Nguru, Malundwe, Rubeho, Udzungwa, and Rungwe Mountains (Stanley et al., 1998a,b; Stanley & Hutterer, 2007; W. T. Stanley, unpubl. data).

ECOLOGY AND REPRODUCTION—In the East Usambara, seven of eight specimens collected were taken in the control site in either undisturbed or only slightly disturbed forest. The single exception was an individual in the 0.2B-ha fragment, an isolated block of heavily disturbed forest. Specimens were obtained in terrestrial or arboreal trap sets, reflecting mixed substrate use. Of the three animals captured in arboreal trap sets, all were in Victor Traps. Placements included: at a 15° angle, about 25 cm off the ground and on a 4-cm-diameter vine; at a 30° angle, approximately 2 m above the ground and across two vines (6 and 13 cm diameter) growing around a tree; and at a 30° angle, 1.5 m off the ground and on a 1-cm-diameter vine. In the latter two cases, the animals were climbing up vines. Two males were found in pitfall buckets; one was found on the dawn trap check after a night of heavy rain. Three specimens were taken in Museum Specials placed on the ground, including a trap next to a tree with a 25 by 10-cm hole at the base (two separate individuals on consecutive nights) and one set in a 20-cm gap between two trees (1.5 and 1 m diameter). The only *Beamys* captured in the West Usambara was in the 5.5-ha fragment with the trap placed on the ground and in thick understory.

In the East Usambara, two males were collected in 1992 with abdominal testes measuring 4 by 2 mm and with non-

TABLE 2. External measurements (mm) and weight (g) of select rodent species collected during 1991–1993 surveys of the East and West Usambara Mountains, including total length (TL), head and body length (HB), length of tail vertebrae (TV), hind foot length (HF), ear length (EAR), and weight (WT). Given differences in measuring techniques between the two field collectors, measurements are presented separately. A one-way analysis of variance was used to test for sexual dimorphism, significant differences between the East and West Usambaras, or both. Only if significant differences were detected are samples presented separately, as well as associated statistical information.

Species	TL	HB	TV	HF	EAR	WT
<i>Paraxerus vexillarius</i> S.M.G., WU, ♀						
Mean ± SD	420.0 ± 25.46		196.0 ± 15.56	56.0 ± 1.0	20.3 ± 2.08	252.7 ± 64.94
Range	402–438		185–207	55–57	18–22	178–296
n	2		2	3	3	3
<i>Dendromus mystacalis</i> S.M.G., EU, ♀, ♂						
Mean ± SD	135.1 ± 12.00	60.0 ± 5.15	74.6 ± 7.33	15.2 ± 1.04	13.0 ± 1.07	5.7 ± 1.55
Range	114–149	51–68	64–86	14–17	11–14	3.5–8.5
n	8	8	8	8	8	8
<i>Dendromus mystacalis</i> W.T.S., EU, ♂						
Mean ± SD	129.7 ± 3.06	59.3 ± 3.06	69.7 ± 2.52	17.0 ± 1.00	10.7 ± 0.58	5.6 ± 0.47
Range	127–133	56–62	67–72	16–18	10–11	5.2–6.1
n	3	3	3	3	3	3
<i>Beamys hindei</i> S.M.G., EU, WU, ♀						
Mean ± SD	274.7 ± 6.90	140.7 ± 6.03	132.7 ± 8.54	22.7 ± 2.06	23.7 ± 2.06	59.5 ± 5.43
Range	269–284	135–147	122–141	20–25	21–26	53–65.5
n	4	4	4	4	4	4
<i>Beamys hindei</i> W.T.S., EU, ♀, ♂						
Mean ± SD	257.0 ± 36.33	135.0 ± 23.80	128.7 ± 11.41	24.7 ± 0.50	22.0 ± 0.82	58.7 ± 25.00
Range	219–291	110–160	114–140	24–25	21–23	38–93
n	4	4	4	4	4	4
<i>Lophuromys aquilus</i> S.M.G., EU, ♀						
Mean ± SD	199.2 ± 10.71	127.3 ± 8.16	68.9 ± 7.11	21.2 ± 1.26	18.8 ± 0.88	60.3 ± 11.07
Range	180–215	109–140	52–77	19–24	17–20	46–89
n	18	14	18	18	18	18
<i>Lophuromys aquilus</i> S.M.G., EU, ♂						
Mean ± SD	198.4 ± 12.16	124.0 ± 6.75	69.2 ± 8.40	21.7 ± 1.59	18.5 ± 1.17	58.0 ± 7.71
Range	172–216	110–137	45–84	18–24	16–20	41.5–73.5
n	28	21	28	28	28	28
<i>Lophuromys aquilus</i> W.T.S., EU, ♀						
Mean ± SD	193.3 ± 12.37	126.5 ± 7.29	69.6 ± 7.77	23.4 ± 1.03	17.5 ± 0.87	57.6 ± 10.99
Range	174–216	111–140	54–84	22–25	15–19	42–87
n	21	21	21	21	21	21
<i>Lophuromys aquilus</i> W.T.S., EU, ♂						
Mean ± SD	190.5 ± 10.84	124.6 ± 7.27	67.6 ± 4.40	23.5 ± 0.88	17.0 ± 0.84	57.6 ± 10.99
Range	172–214	110–137	59–77	22–25	14–18	42–87
n	28	28	28	28	28	21
<i>Lophuromys aquilus</i> S.M.G., WU, ♀						
Mean ± SD	198.0 ± 10.06	127.0 ± 7.07	66.9 ± 5.29	22.6 ± 1.40	18.6 ± 1.09	56.0 ± 8.20
Range	180–214	122–132	57–78	20–24	16–20	45.5–72
n	14	2	14	14	14	14
<i>Lophuromys aquilus</i> S.M.G., WU, ♂						
Mean ± SD	191.6 ± 12.98	123.0 ± 4.24	67.4 ± 7.63	22.3 ± 1.13	18.5 ± 1.51	52.8 ± 8.26
Range	169–210	120–126	47–78	20–24	17–23	40–69
n	16	2	16	16	14	16
<i>Lophuromys aquilus</i> W.T.S., WU, ♀						
Mean ± SD	191.5 ± 14.85	123.0 ± 9.90	68.0 ± 4.24	23.0 ± 0.00	17.0 ± 1.41	50.3 ± 10.96
Range	181–202	116–130	65–71	23–23	16–18	42.5–58
n	2	2	2	2	2	2
<i>Lophuromys aquilus</i> W.T.S., WU, ♂						
Mean ± SD	198.5 ± 12.02	127.0 ± 8.49	74.0 ± 5.66	22.0 ± 1.41	17.5 ± 0.71	56.0 ± 4.24
Range	190–207	121–133	70–78	21–23	17–18	53–59
n	2	2	2	2	2	2
<i>Aethomys hindei</i> S.M.G., WU, ♂						
	197		89	25	20	38.5
<i>Grammomys ibeanus</i> S.M.G., EU, WU, ♀, ♂						
Mean ± SD	296.0 ± 26.34	124	176.1 ± 17.17	24.2 ± 0.95	18.9 ± 1.37	44.4 ± 9.37
Range	240–361		140–220	22–26	17–21	27.5–60
n	19		20	20	19	19

TABLE 2. *Continued.*

Species	TL	HB	TV	HF	EAR	WT
<i>Grammomys ibeanus</i> W.T.S., EU, WU, ♀, ♂						
Mean ± SD	300.2 ± 14.13	121.4 ± 7.54	168.6 ± 24.11	24.6 ± 2.07	19.0 ± 1.22	46.3 ± 6.03
Range	279–315	112–130	129–194	21–26	17–20	39.5–51.5
n	5	5	5	5	5	5
<i>Grammomys macmillani</i> W.T.S., EU, ♀, ♂						
Mean ± SD	254.5 ± 24.46	107.8 ± 10.87	151.3 ± 14.89	23.3 ± 0.50	16.0 ± 1.63	38.9 ± 9.59
Range	230–288	97–119	136–171	23–24	14–18	30–51
n	4	4	4	4	4	4
<i>Grammomys macmillani</i> S.M.G., EU, WU, ♀, ♂						
Mean ± SD	265.1 ± 21.94	112.0 ± 9.38	155.4 ± 13.95	22.6 ± 1.34	17.8 ± 1.17	35.2 ± 9.98
Range	221–297	97–123	125–174	21–25	16–20	17.5–46.5
n	16	6	16	18	18	18
<i>Hylomyscus arcimontensis</i> S.M.G., EU, ♀						
Mean ± SD	221.4 ± 12.27	86.7 ± 7.17	132.7 ± 8.84	18.7 ± 0.78	18.2 ± 0.94	18.4 ± 3.63
Range	194–235	72–92	118–142	17–20	17–20	11–24.5
n	11	8	11	12	12	12
<i>Hylomyscus arcimontensis</i> S.M.G., EU, ♂						
Mean ± SD	225.0 ± 21.52	87.4 ± 10.91	136.0 ± 12.66	19.0 ± 1.00	18.1 ± 0.76	21.4 ± 5.39
Range	194–253	63–105	116–154	17–20	17–19	11–26.5
n	13	12	13	13	13	12
<i>Hylomyscus arcimontensis</i> W.T.S., EU, ♀						
Mean ± SD	231.7 ± 11.09	92.0 ± 5.10	141.6 ± 7.44	20.5 ± 0.71	17.7 ± 0.67	20.0 ± 3.65
Range	208–247	81–100	124–150	20–22	17–19	14–26
n	10	10	10	10	10	9
<i>Hylomyscus arcimontensis</i> W.T.S., EU, ♂						
Mean ± SD	222.9 ± 26.17	91.3 ± 12.22	137.4 ± 13.81	20.8 ± 1.09	17.0 ± 1.00	20.7 ± 5.93
Range	186–262	75–110	120–161	19–22	15–18	12–29
n	8	9	8	9	9	9
<i>Hylomyscus arcimontensis</i> S.M.G., WU, ♀						
Mean ± SD	222.5 ± 9.59	88.3 ± 5.06	134.1 ± 5.97	19.7 ± 0.98	17.8 ± 0.70	17.4 ± 2.72
Range	200–241	77–97	120–147	18–22	17–21	12.5–26.5
n	53	14	53	56	56	56
<i>Hylomyscus arcimontensis</i> S.M.G., WU, ♂						
Mean ± SD	226.5 ± 9.81	92.4 ± 3.97	135.1 ± 6.64	20.1 ± 0.92	17.8 ± 0.98	21.7 ± 4.07
Range	190–249	87–97	110–151	18–22	15–21	14–34
n	52	5	54	54	52	53
<i>Hylomyscus arcimontensis</i> W.T.S., WU, ♀						
Mean ± SD	214.7 ± 9.70	87.2 ± 4.69	130.8 ± 5.69	20.0 ± 0.53	16.5 ± 2.42	16.3 ± 2.35
Range	198–232	80–96	117–141	19–21	8–18	13.5–21
n	14	15	14	15	15	15
<i>Hylomyscus arcimontensis</i> W.T.S., WU, ♂						
Mean ± SD	228.1 ± 10.20	94.7 ± 4.29	138.5 ± 6.81	20.8 ± 0.70	17.0 ± 0.68	21.6 ± 2.50
Range	211–245	87–102	127–151	20–22	16–18	18–25
n	14	14	14	14	14	14
<i>Mus musculoides</i> S.M.G., WU, ♂						
	96		43	12	8	3
<i>Mus musculoides</i> W.T.S., EU, ♂						
	97	58	42	13	9	4.8
<i>Rattus rattus</i> S.M.G., EU, ♂						
	346	155	195	33	22	86
<i>Rattus rattus</i> W.T.S., EU, ♀, ♂						
Mean ± SD	344.0 ± 0.00	159.0 ± 1.41	194.0 ± 1.41	33.0 ± 1.41	21.0 ± 1.41	102.0 ± 1.41
Range	344–344	158–160	193–195	32–34	20–22	101–103
n	2	2	2	2	2	2
<i>Graphiurus kelleni</i> W.T.S., EU, ♂						
	134	79	55	18	13	14.5
<i>Graphiurus murinus</i> W.T.S., EU, WU, ♀, ♂						
Mean ± SD	167.1 ± 14.85	98.6 ± 2.62	71.1 ± 14.61	20.0 ± 1.41	15.0 ± 0.76	22.3 ± 2.67
Range	143–180	94–101	44–83	17–22	14–16	18.5–27
n	8	8	8	8	8	8
<i>Graphiurus murinus</i> S.M.G., WU, ♀, ♂						
Mean ± SD	168.8 ± 12.84	95.5 ± 3.54	79.2 ± 10.67	18.0 ± 1.27	15.1 ± 1.05	19.4 ± 2.56
Range	136–195	93–98	43–93	16–20	14–17	15–25.5
n	17	2	17	17	17	16

TABLE 3. External measurements (mm) and weight (g) of *Praomys delectorum* collected during 1991–1993 surveys of the East and West Usambara Mountains, including total length (TL), head and body length (HB), length of tail vertebrae (TV), hind foot length (HF), ear length (EAR), and weight (WT). Specimens were separated by field collector and sex. F values generated from a one-way analysis of variance are presented.

	TL	HB	TV	HF	EAR	WT
S.M.G.						
East Usambara						
Females						
Mean ± SD	223.7 ± 18.05	98.5 ± 6.67	123.2 ± 11.38	21.2 ± 1.31	20.0 ± 1.07	25.4 ± 5.81
Range	187–251	86–109	99–143	17–23	18–23	14.5–33.5
n	21	19	21	20	21	20
Males						
Mean ± SD	231.8 ± 17.61	103.0 ± 8.81	127.5 ± 10.75	22.5 ± 1.03	20.5 ± 1.17	29.0 ± 7.07
Range	190–262	85–116	104–145	21–24	18–22	15.0–42.5
n	21	20	21	21	21	20
F	2.2	3.2	1.5	13.1***	2.3	3.0
West Usambara						
Females						
Mean ± SD	216.0 ± 14.54		121.3 ± 7.80	21.5 ± 0.58	20.3 ± 0.96	20.5 ± 3.76
Range	196–229		110–128	21–22	19–21	17.5–26
n	4		4	4	4	4
Males						
Mean ± SD	234.1 ± 11.21		129.1 ± 6.23	22.5 ± 0.97	20.5 ± 1.17	24.6 ± 4.06
Range	213–249		118–138	21–25	18–22	15.5–30.5
n	9		10	13	12	12
F	6.1*		4.0	3.5	0.1	3.1
W.T.S.						
East Usambara						
Females						
Mean ± SD	209.7 ± 13.80	96.1 ± 6.63	116.1 ± 7.76	22.8 ± 0.70	18.7 ± 0.98	23.8 ± 6.23
Range	174–228	80–105	98–129	22–24	17–20	14.0–37.5
n	20	20	20	20	20	19
Males						
Mean ± SD	223.5 ± 20.77	101.4 ± 10.63	124.4 ± 11.62	23.7 ± 1.18	18.9 ± 1.05	28.1 ± 6.54
Range	162–258	75–115	90–148	21–26	16–20	14.5–39.5
n	30	33	30	33	33	33
F	6.9*	3.9	7.8**	10.2**	0.4	5.4*
West Usambara						
Females						
Mean ± SD	224.7 ± 7.51	97.8 ± 6.72	116.8 ± 14.38	22.8 ± 1.10	18.6 ± 1.14	22.8 ± 3.72
Range	216–229	90–108	96–135	21–24	17–20	19.5–29.0
n	3	5	5	5	5	5
Males						
Mean ± SD	231.0 ± 9.85	107.0 ± 2.65	127.0 ± 8.19	24.3 ± 1.15	20.3 ± 0.58	30.7 ± 2.25
Range	223–242	105–110	120–136	23–25	20–21	28.5–33.0
n	3	3	3	3	3	3
F	0.8	4.9	1.2	3.5	5.8	10.6*

* P < 0.05.

** P < 0.01.

*** P < 0.001.

convoluted epididymides. Six females were obtained: three with perforate vaginas and three imperforate. Only one out of five females dissected was pregnant (one embryo in the left uterine horn, three in the right, and the largest embryo with a crown-rump length of 6 mm), with five placental scars (two left, three right), and large teats. One of the other four females examined had placental scars (one left, three right) and was lactating. The West Usambara specimen was a nulliparous female.

Two lactating adult females were found on the same day in traps 5 m apart: one was on the ground at the base of a tree and the other on a vine 1.5 m off the ground. The following day, a subadult nulliparous female was captured in the trap set at the base of the tree. One of the *Beomys* captured in 1993 had seven fecal pellets in the large intestine that measured 8 by 5, 8 by 5, 8 by 4, 7 by 4.5, 6 by 4.5, 6 by 4, and 7 by 5 mm.

See Table 2 for external measurements. In the type description of *B. hindei*, Thomas (1909) stated that diagnostic characteristics of this species include six pads on all four feet and the fifth hind toe without a claw. The original description of *B. major* Dollman 1914, with the type series from Mt. Mulanje, Malawi, omits details on the foot pads or claws. However, Hanney and Morris (1962) described these characters from a series of *B. major* collected in Malawi. All 19 adult specimens they examined had six pads on the hind foot and five pads on the forefoot, and every digit had a claw, with the exception of the forefoot pollex with a nail. All of our specimens from the Usambara Mountains had the same claw condition as described for *B. major*. Some authorities consider *major* a subspecies of *B. hindei* (Hubbard, 1970; Ansell & Ansell, 1973; Corbet & Hill, 1991), whereas others suggest the

TABLE 4. Abundance of rodent species in forest fragments sampled in the East Usambara based on the proportional field effort in a given forest block. Results of χ^2 tests compare expected to observed captures for each species in each fragment. Expected trap success is based on the null hypothesis of equal distribution across all fragments. Captures by techniques other than traps (i.e., pitfalls and animals brought to us by local people) are not included. Significantly higher abundance than expected in a given fragment is shown in bold.

Species	Site (trap-nights)										χ^2	
	0.2A (150)	0.4 (75)	0.2B (150)	0.6 (370)	0.8 (300)	3.1 (200)	2.6 (150)	3.3 (460)	29.4 (450)	Control (2837)		Total (5142)
<i>Beamys hindei</i>			1							3	4	8.62
<i>Grammomys macmillani</i>	4			5		1					10	82.88***
<i>Grammomys ibeanus</i>					1					2	3	5.30
<i>Hylomyscus arcimontensis</i>									1	28	29	23.47**
<i>Lophuromys aquilus</i>	4	3	4	6	10	3	2	3	5	45	85	13.27
<i>Mastomys natalensis</i>										1	1	0.81
<i>Praomys delectorum</i>			3		10	4	1	15	13	125	178	24.54**
<i>Rattus rattus</i>									1	3	4	3.06
<i>Graphiurus murinus</i>	1				1					2	4	10.50
Total captures per site	9	3	8	18	22	8	3	18	20	209	318	20.31*
No. of species per site	3	1	3	3	4	3	2	2	4	8	9	

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

two forms may be distinct species (Ellerman, 1941; Hanney, 1965; Musser & Carleton, 2005). A critical study is needed to resolve this question.

SPECIMENS EXAMINED—EAST USAMBARA, 6 km NW Amani, Monga Tea Estate (TRL S—FMNH 150099); 4.5 km WNW Amani, Monga Tea Estate, control site (PF 33—FMNH 150100; TRL AN—FMNH 151223); 4.5 km ESE Amani, Monga Tea Estate, control site (PF 41—FMNH 150101; TRL AF—FMNH 150102, 150103, 150428; TRL AP—FMNH 151224); WEST USAMBARA, 11 km NW Korogwe, Ambangulu Tea Estate (TRL F—FMNH 147238).

Family Muridae: Subfamily Deomyiinae

Lophuromys aquilus True, 1892

DISTRIBUTION—*Lophuromys aquilus* was previously referred to in the literature as *L. flavopunctatus* Thomas, 1888 (Verheyen et al., 2002; Musser & Carleton, 2005). *Lophuromys aquilus* has a broad distribution in lowland and mesic montane habitats in eastern and some central African countries (including Democratic Republic of the Congo) and extends as far south as Angola. In Tanzania, it is found on most massifs with montane forests, except Mt. Meru, where the endemic *L. verhageni* W. Verheyen, Hulselmans, Dierckx and E. Verheyen, 2002, occurs; this latter species was also previously included within *L. flavopunctatus* (Musser & Carleton, 2005).

ECOLOGY AND REPRODUCTION—*Lophuromys aquilus* was among the most commonly trapped rodents in the East Usambara forests, second only to *Praomys delectorum*, and making up 26% of the total murids captured (Table 4). Capture rates of *L. aquilus* varied among sites; it was the most abundant rodent in fragments less than 5 ha, the second most abundant species in the 3.3- and 29.4-ha parcels, and ranked third in the control area.

Lophuromys aquilus was less abundant (based on trap success) in the West Usambara, compared with the East Usambara (Table 4), where it made up 12.4% of the total murids captured, exceeded by *P. delectorum* and *Hylomyscus arcimontensis*. The 1.9-ha fragment was the only forest site where *L. aquilus* was the most abundant trapped rodent; in the other parcels less than 5 ha, it was the second most abundant

species. At the 37.8-ha and control sites, this species was distinctly less common.

Overall, 173 specimens were collected during this study, and with the exception of five individuals either captured by hand, tangled in a mist net, or found in a pitfall, all were in the trap lines. All trap sets that yielded this species were either on the ground or on slightly elevated surfaces with direct non-vertical access from the ground. There is no evidence of scansorial displacement in this species. *Lophuromys* was frequently captured in areas with moist soil and thick herbaceous vegetation. In 30 cases, two individuals were captured in the same trap set, and in five cases, three individuals were obtained in the same trap set.

Of the 173 animals captured, only four individuals were not sexed. The ratio of females to males was 78:91. Over the study, 26 females were examined for reproductive activity (four, 19, and three in 1991, 1992, and 1993, respectively); six (23.1%) were pregnant (1 [25%], 4 [21%], 1 [33%], respectively). The crown-rump length of the embryos ranged from 3 to 32 mm (mean = 20.8 mm). The testes of 32 males were examined, and the mean measurements were 9.4 by 6.0 mm, and 24 of 31 assessed (77%) had convoluted epididymides. In a sample from the West Usambara measured by S.M.G., the hind foot lengths of the males were significantly larger than those of females ($F = 8.1$, $P < 0.01$; Table 2). Based on this result, in Table 2, the external measurements are separated by sex and further subdivided by mountain and collector.

COMMENTS—Cunneyworth et al. (1996) reported captures of *Lophuromys sikapusi* (Temminck, 1853) at several sites in the Magoroto Forest Reserve, East Usambara, but listed no voucher specimens. The species name *L. sikapusi* was previously used for members of this genus occurring in the region (Swynnerton & Hayman, 1951), but after recent taxonomic changes, these records are almost certainly referable to *L. aquilus*.

SPECIMENS EXAMINED—EAST USAMBARA, 6 km NW Amani, Monga Tea Estate (TRL O—FMNH 150206, 150456, 150457, 150460; TRL P—FMNH 150459; TRL Q—FMNH 150207, 150458; TRL R—FMNH 150171, 150172, 150205, 150453, 150454, 150461; TRL S—FMNH 150173, 150179, 150208, 150464; TRL T—FMNH 150174–150178, 150455, 150462, 150465, 150466, 150471; TRL U—

FMNH 150463, 150467–150470; TRL W—FMNH 150180, 150181); 8 km NWN Amani, Bulwa Tea Estate (TRL AA—FMNH 150191, 150192, 150488; TRL AB—FMNH 150195, 150213, 150486; TRL AC—FMNH 150193, 150485; TRL AD—FMNH 150194, 150487, 150489, 150490); 4.5 km WNW Amani, Monga Tea Estate, control site (TRL M—FMNH 147303, 147509, 147512, 147513; TRL N—FMNH 147304, 147510, 147511, 147514; TRL X—FMNH 150479, 150482, 150483, 151483; TRL Y—FMNH 150182, 150183, 150185, 150186, 150209, 150210, 150472, 150473; TRL Z—FMNH 150184, 150187, 150189, 150190, 150211, 150474–150478, 150480, 150481; TRL AN—FMNH 151484, 151485; TRL AO—FMNH 151256, 151257, 151260, 151490, 151491; captured by hand—FMNH 150188, 150212); 4.5 km ESE Amani, Monga Tea Estate, control site (PF 64—FMNH 151494; TRL AF—FMNH 150196; TRL AG—FMNH 150197–150199, 150491; TRL AH—FMNH 150200–150202, 150492–150495; TRL AJ—FMNH 150496–150504; TRL AP—FMNH 151258, 151486, 151487, 151492, 151493; TRL AQ—FMNH 151255, 151262, 151488, 151489; captured by hand—FMNH 151261); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 4—FMNH 147491; TRL A—FMNH 147292, 147478; TRL G—FMNH 147293, 147479, 147481, 147483–147485; TRL H—FMNH 147295, 147480, 147482, 147486, 147489; TRL I—FMNH 147294, 147487, 147490; TRL K—FMNH 147297, 147298, 147494–147498, 147500, 147501, 147503; TRL L—FMNH 147301, 147504; TRL AK—FMNH 150214, 150215, 150506–150508; TRL AL—FMNH 150203, 150204; TRL AR—FMNH 151481, 151482); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147296, 147492, 147493, 147499, 147502); 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147299, 147506, 147507; TRL E—FMNH 147300, 147505; TRL F—FMNH 147302, 147508).

Family Muridae: Subfamily Murinae
***Aethomys hindei* (Thomas, 1902)**

DISTRIBUTION—*Aethomys hindei* has been reported from throughout eastern Africa, and as far west as Chad. It is not known south of Tanzania (Musser & Carleton, 2005). Kingdon (1974a) stated that this species is “certainly not a forest animal” but a grassland species. However, it has been captured in fallow areas at the edge of forests (Hubbard, 1972). Davis (1975) suggested that two morphological forms of *A. hindei* were found on either side of the Eastern Rift Valley. Swynnerton and Hayman (1951) considered *hindei* as a subspecies of *kaiseri* (Noack, 1887) and mentioned records from Amani and Magoroto (in the Tanga Region) and from Kibongoto (near Mt. Kilimanjaro). *Aethomys hindei* is also reported from Muheza village at the southeastern base of the East Usambara and in distinctly drier habitat (Hubbard, 1972).

ECOLOGY AND REPRODUCTION—The single animal referable to this species we captured in the Usambara Mountains was a juvenile male taken in the West Usambara 1.9-ha fragment at 1171 m in disturbed montane forest. It was obtained in a Museum Special trap placed on the ground in leaf litter and slightly less than 100 m from the forest edge. The animal was found in the trap at 1500 h, suggesting diurnal activity. The testes were abdominal, measuring 4 by 2 mm, with non-convoluted epididymides.

In the Usambaras, *A. hindei* is unknown in undisturbed forest, and it is unclear to what extent it occurs at higher elevations in agricultural areas. Hubbard (1972) collected this species in July at 200 m in Muheza at the base of the East Usambara. Of the 16 females he obtained, 25% were pregnant. Table 2 reports external measurements of our trapped individual.

COMMENTS—The single individual captured was a juvenile and based on cranio-dental measurements and characters it falls within the range of *A. hindei* (sensu Davis, 1975; see also Denys & Tranier, 1992). The incisors are opisthodont, the greatest length of the skull (30.5 mm) minus the condylobasal length (27.6 mm) is 2.9 mm, and the zygomatic width is 53% of the greatest length of the skull. We echo the call for a systematic review of the genus to define species limits of *A. kaiseri* and *A. hindei* (Musser & Carleton, 2005).

SPECIMENS EXAMINED—**WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (TRL E—FMNH 147239).

***Grammomys ibeanus* (Osgood, 1910)**

DISTRIBUTION—*Grammomys ibeanus* is known from north-eastern Zambia to southern Sudan; it is found in different montane forests of eastern Tanzania, but the taxonomy of this presumed species group needs critical review (Stanley et al., 1998b; Musser & Carleton, 2005).

ECOLOGY AND REPRODUCTION—A substantial proportion of the total 25 trapped individuals (13 females and 12 males) was obtained in the control sites of the East (66%) and West Usambaras (41%). In the East Usambara, three specimens were collected: two in the EU control site forest and the third in the 0.8-ha fragment. In the West Usambara, six were collected in the 1.5-ha fragment, four in the 5.5-ha fragment, three in the 37.8-ha fragment, and nine in the WU control site. Within the different habitats sampled in the WU control site, four *G. ibeanus* were collected in TRL H, placed in an area at the forest edge that had recently been cut and colonized by secondary vegetation; four in TRL B and TRL AR, characterized by relatively dry but pristine forest; and one in TRL AK with primary forest. We did not observe sympatric occurrence in the same forest fragment of *G. ibeanus* and *G. macmillani*.

In general, traps set on limbs associated with thick vegetation or trees were particularly successful in capturing *G. ibeanus*. Ground sets on moist soil in thick secondary and herbaceous vegetation were also productive. On more than one occasion, specimens were caught on consecutive nights in the same trap or neighboring traps. For example, in 1991, in the 37.8-ha West Usambara fragment, two females and one scrotal male were captured on two consecutive nights in Museum Specials set on 5–10-cm-diameter vines 1.5–2 m off the ground. All of these traps were within 30 m of the forest edge. In 1992, in the EU control site (TRL AH), two specimens of *G. ibeanus* were trapped on consecutive nights in the same Museum Special set on the ground—the first night (23 August 1992) a scrotal male and the following night a female without embryos or placental scars and with a perforated vagina. In the WU control site, in the TRL H line placed in secondary vegetation, four specimens were caught in the course of five consecutive nights in Museum Specials (two in the same trap) within 11 m from each other. In 1993, in the TRL AR line in the WU control site, two females (one nulliparous and one with eight placental scars) were taken on 20 August in two consecutive Museum Specials.

Of the two females collected in the East Usambara Mountains, one was nulliparous and the other, captured in the 0.8-ha fragment, had two embryos in the left and one in the right uterine horns, the largest of which was 10 mm in crown-rump length. The one male had scrotal testes that measured 15 by 10 mm and convoluted epididymides. In the

West Usambara, none of five females checked was pregnant, and of the four examined for previous reproductive activity, three had two and two, two and three, and two and six placental scars in the left and right uterine horns, respectively. The fifth individual was nulliparous.

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL T—FMNH 150105); 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AH—FMNH 150106, 150107); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147246, 147248, 147415, 147418, 147420, 147422; TRL F—FMNH 147247, 147416, 147417, 147419); 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL H—FMNH 147240–147242, 147405; TRL B—FMNH 147244, 147410; TRL AK—FMNH 150108; TRL AR—151235, 151236); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147245, 147412, 147413).

Grammomys macmillani (Wroughton, 1907)

DISTRIBUTION—*Grammomys macmillani* is reported from Sierra Leone to Tanzania and south to Zimbabwe, but the precise geographical limits of its distribution are unresolved (Musser & Carleton, 2005). Within Tanzania, the species has been found in both lowland (e.g., Minziro Forest) and montane forest localities (South Pare) (Stanley et al., 1998a; Stanley & Foley, 2008). Matschie (1915) described *G. m. usambara* based on a specimen collected in Amani in 1911.

ECOLOGY AND REPRODUCTION—In total, 22 specimens were obtained in the East and West Usambaras during this study. Seven females and four males were captured in the East Usambara, and five females and four males (for two specimens, the sex was not determined) in the West Usambara. In contrast to *G. ibeanus* (see above), which was often found in large, relatively non-degraded forest fragments, all specimens of *G. macmillani*, with one exception, were captured in forest fragments under 2 ha or in disturbed habitat. The exception was an individual trapped in PF 3 in the WU control site forest. In the East Usambara, five of the 11 (45%) were captured in the 0.6-ha fragment, four (36%) in the 0.2A-ha fragment, one in the 3.1-ha fragment, and one in PF 57 placed in tea habitat. In the West Usambara, six of the 11 collected (55%) were in TRL I, and single individuals were captured in TRL J and PR 10 (both in the 1.8-ha fragment), and TRL H and PF 3 (both in the WU control site).

Whereas *G. ibeanus* was obtained almost exclusively in arboreal sets, *G. macmillani* seems to be more terrestrial in its substrate use. However, four of the 11 (36%) individuals of *G. macmillani* caught in the East Usambara were in traps set 1–2.5 m above the ground, whereas in the West Usambara, two of the 11 (18%) specimens captured were taken in arboreal sets. In the 0.2A - and 0.6-ha fragments of the East Usambara, traps on the ground that yielded *G. macmillani* include Museum Specials set next to logs, tree buttresses, or vine tangles and placed either on the forest edge or toward the interior of the fragment. Traps set in thick vegetation, consisting of both woody and herbaceous vines, were particularly productive for this species. Ecotonal areas between forest and agricultural land, such as TRL I produced numerous individuals of *G. macmillani*.

All but one of the seven females of *G. macmillani* captured in the East Usambara sites were pregnant or had evidence of past pregnancies. Four had four and zero, one and two, zero and five, and three and one embryos in the left and right uterine horns, the largest having crown–rump lengths of 17, 24, 10, and 5 mm, respectively. Two non-pregnant females had

two and zero and three and two placental scars in the left and right uterine horns, respectively. The remaining individual was nulliparous. Only one of five females captured in the West Usambara sites was examined, and it was nulliparous. The reproductive status of three of four males captured in the East Usambara was assessed: one had abdominal testes (8 by 4 mm), and two had scrotal testes (9 by 6 and 8 by 4 mm). All had non-convoluted epididymides. Four males collected in the West Usambara were examined for reproductive condition: one had scrotal testes (9 by 3 mm), and three had abdominal testes, one of which measured 6 by 4 mm. See Table 2 for external measurements.

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL O—FMNH 150111–150114; TRL R—FMNH 150109, 150110, 150115, 150116, 150372; TRL AA—FMNH 150117); 4.5 km WNW Amani, Monga Tea Estate, control site (PF 57—FMNH 151476); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147414; TRL E—FMNH 147421); 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 3—FMNH 147404; TRL G—FMNH 147249, 147406; TRL I—FMNH 147250, 147408, 147409, 147411; TRL J—FMNH 147243; TRL H—FMNH 147407).

Hylomyscus arcimontensis Carleton & Stanley, 2005

DISTRIBUTION—This species is distributed across montane islands throughout eastern and southern Tanzania and may extend into northern Malawi (Carleton & Stanley, 2005). Within Tanzania, *H. arcimontensis* occurs on all Eastern Arc Mountains (and Mt. Rungwe) but is not known from the Taita Hills of Kenya or from geologically recent northern volcanoes such as Mt. Kilimanjaro and Mt. Meru.

ECOLOGY AND REPRODUCTION—Over the three-year study in the Usambaras, 187 specimens of *H. arcimontensis* were captured, including 45 in the East and 141 in the West, which composed 9.9% and 21.3% of the total rodents captured on each massif, respectively. This species was the third and second most common rodent in the East and West Usambara Mountains, respectively.

The large samples of this taxon collected on each massif allow for the examination of patterns of sexual and geographic variation. A one-way analysis of variance was computed to determine whether this species shows sexual dimorphism in external measurements. More than 50 specimens of each sex were measured by S.M.G. in the West Usambara in 1991 and 1992. Males were larger than females in total length ($F = 4.4$, $P = 0.04$) and weight ($F = 41.7$, $P < 0.0001$). Tail, hind foot, and ear length measurements did not differ significantly between the sexes. Measurements recorded by S.M.G. from both the East and West Usambaras were compared for differences between the massifs. Total length and hind foot length were larger in females from the West than females from the East ($F = 12.6$, $P < 0.001$), and a similar pattern for the same variables was found in males ($F = 19.3$, $P < 0.0001$). Descriptive statistics for measurements divided by sex, collector, and massif are presented in Table 2.

COMMENTS—Almost all of the specimens from the East Usambara were collected in the EU control site, suggesting microhabitat preferences, related presumably to forest size and vegetation composition. The single exception was an animal (FMNH 150139) captured in a tea plantation approximately 30 m from the 0.6-ha fragment that may have been dispersing between forest blocks. Abundance of this species, as measured by trap success, was notably lower on other Eastern Arc

Mountains (compared with the Usambaras) which possess relatively smaller amounts of remaining natural forest, such as the North Pare and Nguu Mountains (Stanley et al., 2007a; W. T. Stanley, unpubl. data).

SPECIMENS EXAMINED—EAST USAMBARA, 6 km NW Amani, Monga Tea Estate (TRL U—FMNH 150118; TRL V—FMNH 150139); 4.5 km WNW Amani, Monga Tea Estate, control site (TRL M—FMNH 147290, 147291, 147475, 147477; TRL N—FMNH 147476; TRL X—FMNH 150119; TRL AO—FMNH 151240, 151251); 4.5 km ESE Amani, Monga Tea Estate, control site (PF 41—FMNH 150141; TRL AF—FMNH 150140, 150142; TRL AG—FMNH 150143, 150429–150431, 150435; TRL AH—FMNH 150120–150125, 150147, 150148, 150432–150434; TRL AI—FMNH 150144–150146, 150149–150153, 150436; TRL AP—FMNH 151250, 151252, 151480; TRL AQ—FMNH 151246–151248, 151479); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL A—FMNH 147251, 147425–147427, 147431, 147432; TRL B—FMNH 147253–147258, 147262–147264, 147274–147277, 147333, 147435–147439, 147443, 147444, 147447–147453; TRL G—FMNH 147442, 147445; TRL H—FMNH 147252, 147259–147261, 147265–147270, 147423, 147424, 147428–147430, 147433, 147434, 147440, 147441, 147454–147456, 147459–147466, 147468; TRL I—FMNH 147271–147273, 147446; TRL J—FMNH 147457, 147458; TRL AK—FMNH 150154, 150156, 150159–150164, 150166, 150169, 150170, 150448–150452; TRL AL—150126–150138, 150155, 150167, 150168, 150437–150447; TRL AR—151243–151245, 151478); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147278–147289, 147469–147473, 147642); 11 km NW Korogwe, Ambangulu Tea Estate (TRL F—147474).

Mastomys natalensis (Smith, 1834)

DISTRIBUTION—*Mastomys natalensis* is distributed across much of sub-Saharan Africa. This species is ubiquitous in lowland agricultural areas across Tanzania and is a crop pest.

ECOLOGY AND REPRODUCTION—All 13 specimens collected during this study were captured on the ground, and 12 specimens were caught in 1991 in the West Usambara. Ten animals were collected in TRL G, placed in a fallow agricultural area. A female and a scrotal male were taken on two consecutive days in adjacent Victor Traps in TRL I (the Grid site line) in an area with thick vegetation next to a small rock outcrop. No other habitat sampled in the WU resulted in the capture of *Mastomys*. One specimen was collected in 1992 in the EU control site in TRL AF within closed canopy forest and with an open understory. This reproductively active male was taken 43 m from the forest edge in a Museum Special set in a subterranean root tangle, 50 cm below the level of the ground. This record is atypical, particularly given that we caught no other individual of this rodent in the East Usambara, and those obtained in the West Usambara were all captured in disturbed habitats.

Two of the 13 specimens were not sexed, and the one female examined had a perforate vagina and large mammae. Seven of the nine males captured had scrotal testes measuring 7–15 by 4–8 mm, and four individuals had convoluted epididymides.

SPECIMENS EXAMINED—EAST USAMBARA, 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AF—FMNH 150104); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL G—FMNH 147305–147308, 147515–147517, 147538, 147589, 147590; TRL I—FMNH 147329, 147518).

Mus musculoides Temminck, 1853

DISTRIBUTION—*Mus musculoides* occurs across much of sub-Saharan Africa but is unknown in the southern African

subregion, where it is replaced by *M. minutoides* Smith, 1834 (Musser & Carleton, 2005; but see Veyrunes et al., 2005).

ECOLOGY AND REPRODUCTION—Two males were captured during this study in 1991 and 1992: one in the West Usambara in a *Eucalyptus* plantation and one in the East Usambara in a tea plantation. External measurements are given in Table 2.

SPECIMENS EXAMINED—EAST USAMBARA, 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 150216); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147519).

Praomys delectorum (Thomas, 1910)

DISTRIBUTION—*Praomys delectorum* is distributed within the Tanganyika–Nyasa Montane Forest formation (Moreau, 1966), including montane ranges in Zambia, Malawi, Tanzania, and southeastern Kenya (Musser & Carleton, 2005). Within Tanzania, it is known from all Eastern Arc Mountains, as well as northern volcanoes (Kilimanjaro, Meru, Ngorongoro) and within the Southern Highlands, but does not occur in mountains associated with the Albertine Rift, such as Mahale or Mbizi, where *P. jacksoni* de Winton, 1897, is found (Stanley et al., 1998b; Musser & Carleton, 2005). *Praomys delectorum* has been recorded as low as 300 m in forests at the foot of the East Usambara (Stanley et al., 2005).

ECOLOGY AND REPRODUCTION—To assess whether sexual dimorphism exists in external measurements of *Praomys delectorum*, samples collected from the East and West Usambaras, segregated by collector, were tested for significant differences (Table 3). Males were larger than females in all compared variables. These differences were significant in measurements recorded by both S.M.G. and W.T.S. for the hind foot length in the East Usambara sample; by W.T.S. for total length, tail length, and weight for the East Usambara sample; by S.M.G. for total length for the WU sample; and by W.T.S. for weight for the WU sample. Based on these results, the sexes are separated in statistical comparisons between mountains.

Only one of 17 females (5.9%) examined over the three-year survey was pregnant; this animal was one of 10 dissected in 1991 and had a single embryo in the left and three embryos in the right uterine horn, with the largest crown–rump length at 5 mm. In 1992, seven females were examined for reproductive condition and not a single individual in 1993. No lactating females were recorded.

The testes of 15 males were measured in 1991; the average measurements were 12.0 mm \pm 2.9 (range = 5–17) by 6.1 mm \pm 1.6 (range = 2–8). Thirteen of the 17 individuals had convoluted epididymides. In 1992, 16 males were examined, and the average measurements were 13.7 mm \pm 1.8 (range = 11–17) by 7.1 mm \pm 1.0 (range = 6–9). All had convoluted epididymides. In 1993, the average testes measurements of five males examined were 11.0 mm \pm 3.3 (range = 6–14) by 6.6 mm \pm 2.1 (range = 3–8), and four of five had convoluted epididymides.

In a study conducted between 2004 and 2006, Makundi et al. (2006) found a significant density increase in *Praomys delectorum* sampled in the Magamba Forest, West Usambara, between March and June compared with between September and December. The greatest number of males with scrotal testes and females with perforate vaginas were found from April to June. Based on these observations, as well as our data, little reproductive activity occurs during the dry period (July–

August), this species apparently has a relatively narrow period of annual breeding.

SPECIMENS EXAMINED—EAST USAMBARA, 6 km NW Amani, Monga Tea Estate (TRL P—FMNH 150217–150219, 150221, 150224, 150514, 150515; TRL Q—FMNH 150295, 150297, 150299–150301, 150511–150513; TRL R—FMNH 150220, 150292–150294, 150296, 150298; TRL S—FMNH 150225, 150226, 150509; TRL T—FMNH 150222, 150223, 150303–150307, 150516, 150517, 150519; TRL U—FMNH 150308–150315, 150520–150524); 8 km NWN Amani, Bulwa Tea Estate (TRL AA—FMNH 150332, 150333, 150540, 150541; TRL AC—FMNH 150257); 4.5 km WNW Amani, Monga Tea Estate, control site (TRL M—FMNH 147337, 147576–147578; TRL N—FMNH 147336, 147338; TRL X—FMNH 150231, 150316, 150318–150330, 150536–150539, 151278, 151282; TRL Y—FMNH 150228, 150229, 150232, 150245, 150246, 150249–150252, 150529, 150530; TRL Z—FMNH 150227, 150230, 150233–150236, 150238–150244, 150247, 150248, 150253–150256, 150525–150528, 150531, 150532, 150534, 150535; TRL AM—FMNH 151284, 151309; TRL AN—FMNH 151276, 151277, 151280, 151281, 151283, 151515, 151516, 151518–151527; TRL AO—FMNH 151297–151301, 151308, 151517, 151529); 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AF—FMNH 150265, 150336–150340, 150552, 150559–150561, 150563, 150564, 150570; TRL AG—FMNH 150258–150264, 150334, 150542–150551, 150562, 150565–150569, 150573; TRL AH—FMNH 150266–150279, 150553–150558; TRL AI—FMNH 150341, 150342, 150344–150349; TRL AJ—FMNH 150343, 150571, 150572; TRL AP—FMNH 151285, 151302–151307, 151530–151533; TRL AQ—FMNH 151279, 151286–151296, 151310); **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL A—FMNH 147309–147312, 147314, 147315, 147521–147523, 147527–147529, 147531, 147543; TRL B—FMNH 147317–147319, 147321–147323, 147325, 147330–147332, 147533–147537, 147541, 147542, 147545–147556, 147559, 147560; TRL G—FMNH 147313, 147539, 147540, 147557; TRL H—FMNH 147316, 147320, 147326, 147524–147526, 147530, 147532, 147544; TRL I—FMNH 147558, 147563, 147564; TRL J—FMNH 147324, 147327, 147328, 147561, 147562; TRL K—FMNH 147569–147571; TRL AK—FMNH 150157, 150158, 150165, 150350–150355, 150357–150362, 150583–150601; TRL AL—FMNH 150280–150291, 150356, 150574–150582; TRL AR—FMNH 151271, 151272, 151274, 151275, 151502–151512); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147334, 147565–147568, 147572, 147573); 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147335, 147575; TRL F—FMNH 147574).

Rattus rattus (Linnaeus, 1758)

DISTRIBUTION—As in other areas of east Africa, Tanzanian populations of this introduced species are found in areas associated with human habitation and only occasionally in natural forest.

ECOLOGY AND REPRODUCTION—*Rattus* was rarely captured during our surveys in the Usambaras; only four specimens were taken during the three years. These four were obtained in the East Usambara between 25 July and 3 August 1992, along creeks with running water, in settings similar to where the species was trapped at 300 m in Kwamgumi Forest Reserve at the base of the East Usambara (Stanley et al., 2005). In the 29.4-ha parcel, one specimen was taken in a Victor Trap placed on a flat rock in a streambed within 130 m of the forest edge. Three others were collected in two Victor Traps and one Museum Special in a forested area dominated by the invasive tree *Maesopsis* and within a 32-m stretch of a 358-m-long trap line. All traps successful for this genus were on the ground, in the understory, and in areas with moist soil and thick herbaceous vegetation. Three males and one female were collected, and two of the males were examined for reproduc-

tive activity: one was scrotal and the other, a juvenile, had abdominal testes. External measurements of these animals are presented in Table 2.

COMMENTS—*Rattus* was notably uncommon in natural forests of the Usambaras, as is the case in other montane forests of Tanzania (Stanley et al., 2005; Stanley & Hutterer, 2007; Mulungu et al., 2008; W. T. Stanley, unpubl. data). Matschie (1915) described *R. r. rattiformis* from Amani.

SPECIMENS EXAMINED—EAST USAMBARA, 4.5 km WNW Amani, Monga Tea Estate, control site (TRL Z—FMNH 150602, 150603, 150605); 6 km NW Amani, Monga Tea Estate (TRL U—FMNH 150604).

Family Gliridae: Subfamily Graphiurinae *Graphiurus kelleni* (Reuvens, 1890)

DISTRIBUTION—*Graphiurus kelleni* is known from savannah habitats across much of sub-Saharan Africa, from Senegal to Somalia and south to Mozambique (Holden, 2005). Within Tanzania, it has been previously reported in the Kwamgumi Forest Reserve at 230 m at the foot of the East Usambara (Stanley et al., 2005) and at Kibongoto at 1290 m on the slopes of Mt. Kilimanjaro (Swynnerton & Hayman, 1951).

ECOLOGY AND REPRODUCTION—One male was collected in the control area of the East Usambara in 1993. The animal was obtained in a Museum Special set in an area of open understory, approximately 25 cm off the ground, and on a large tree buttress that extended into the upper canopy. The trap was about 170 m from the forest edge. The animal's testes were abdominal and measured 4 by 2 mm, and the epididymides were non-convoluted.

COMMENTS—The single specimen, an adult, was identified to species based on its small size and blond fur coloration and was confirmed by comparison with other FMNH specimens of *G. kelleni* from the Arusha area identified by M. E. Holden. The only example of this species was taken in the EU control site, where it occurs in sympatry with *G. murinus*.

SPECIMENS EXAMINED—EAST USAMBARA, 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AQ—FMNH 151364).

Graphiurus murinus (Desmarest, 1822)

DISTRIBUTION—*Graphiurus murinus* is found in eastern, central, and southern Africa, from Ethiopia south to South Africa, and as far west as Democratic Republic of Congo (Holden, 2005).

ECOLOGY AND REPRODUCTION—*Graphiurus murinus* was trapped in nearly equal proportions with arboreal (often in the same traps that yielded *Grammomys ibeanus*, *G. macmillani*, and *Hylomyscus arcimontensis*) and ground sets. In the East Usambara, three specimens of *Graphiurus murinus* were collected in three different arboreal sets and two ground sets. Terrestrially placed traps that yielded this species included a Victor Trap at the base of a tree with a hole in the 0.2A-ha fragment, and a Victor Trap next to a buttress of a large tree in the EU control site. The arboreal sets included a Museum Special wedged between a 1-m-diameter tree and a 7-cm-diameter stump about 35 cm off the ground in the 0.8-ha fragment. Two arboreal sets in the EU control area included a Museum Special oriented at 60° on a 4-cm-diameter vine circling a 50-cm-diameter tree, 1.5 m above the ground, and a Museum Special placed 1.3 m off the ground in an 80 by 10-cm hole in the side of a 30-cm-diameter tree.

In the West Usambara, *G. murinus* was captured in the 37.8-ha fragment and the WU control area (both in forest and on the edge of disturbed habitat), but not in the smaller forest fragments. Successful ground sets were in dense growth of bracken fern at the ecotone between forest and fallow agricultural land, inside hollows at the base of trees, and next to or under large rocks. Two males were captured at Ambangulu in 1992 over three consecutive nights in traps set 1 m apart and in close vicinity to exposed rocks. Successful arboreal trap sets in the West Usambara include those in large shrubs and on horizontal limbs ranging from 5 to 30 cm diameter, some surrounded by thick vegetation and others spanning open understory.

Three specimens of each sex were captured in the East Usambara between 1992 and 1993, and all were dissected to ascertain reproductive condition. No female was pregnant; one showed evidence of previous reproduction (one placental scar in the right uterine horn). The three males had abdominal testes measuring 4–6 by 2–3 mm with non-convoluted epididymides.

Fifteen specimens were collected in the West Usambara in 1991 (six males, nine females). Three females showed no signs of active reproduction; one had placental scars (three in the left uterine horn, one in the right). The testes of the four males examined were abdominal and measured 3–5 mm by 2–3 mm, and the epididymides were non-convoluted. Three males collected in 1992 were not scrotal, testes measured 4–10 by 2–4 mm, and the epididymides were non-convoluted. The two specimens captured in 1993 were female, and the single individual dissected was nulliparous.

COMMENTS—One-way analyses of variance found no significant differences between the sexes in external measurements taken by a single collector (Table 2). The only significant difference between populations in the East and West Usambaras was the hind foot length (EU mean = 20.6 mm, $n = 5$; WU mean = 18.1, $n = 20$; $F = 14.6$, $P < 0.001$) and weight (EU mean = 23 g, $n = 5$; WU mean = 19.7, $n = 19$; $F = 6.3$, $P < 0.05$). We attribute these differences to the small sample size from the EU, and, in the case of the hind foot length, difference in measurement techniques between field collectors (see Stanley et al., this volume b). The descriptive statistics for these comparisons are presented in Table 2.

SPECIMENS EXAMINED—EAST USAMBARA, 6 km NW Amani, Monga Tea Estate (TRL O—FMNH 150363; TRL T—FMNH 150364); 4.5 km ESE Amani, Monga Tea Estate, control site (TRL AF—FMNH 150365; TRL AG—FMNH 150366; TRL AP—FMNH 151363); WEST USAMBARA, 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147345, 147346); 12.5 km NW Korogwe, Ambangulu Tea Estate (TRL A—FMNH 147339, 147579, 147581; TRL B—FMNH 147583; TRL H—FMNH 147340–147343; TRL I—FMNH 147344, 147584; TRL AK—FMNH 150367–150369; TRL AR—FMNH 151362, 151542).

Family Bathyergidae: Subfamily Bathyerginae
***Heliophobius argenteocinereus* Peters, 1846**

DISTRIBUTION—*Heliophobius argenteocinereus* is only known from eastern and central Africa, from Zimbabwe to Tanzania and as far west as the Democratic Republic of the Congo, but it appears absent from Uganda (Kingdon, 1974a).

ECOLOGY AND REPRODUCTION—Seven specimens (three females, four males) were collected in the West Usambara between 19 and 22 July 1991, and two females were collected in the East Usambara on 21 July and 12 August 1992. All

animals were taken in agricultural fields, where the species is considered a pest. Table 2 reports external measurements.

From the 1991 collections, the testes of two males were 10 by 6 mm and 10 by 7 mm, and the epididymides of both animals were convoluted; the single female dissected had no embryos, but two placental scars in each uterine horn. The female collected 21 July 1992 was not pregnant, but the individual from 12 August of the same year had three embryos in each uterine horn, the largest of which had a crown–rump length of 6 mm.

SPECIMENS EXAMINED—EAST USAMBARA, 6 km NW Amani, Monga Tea Estate (captured by hand—FMNH 150370); 8 km NWN Amani, Bulwa Tea Estate (captured by hand—FMNH 150371); WEST USAMBARA, 14.5 km NW Korogwe, Ambangulu Tea Estate (captured by hand—FMNH 147347–147349, 147586); approximately 14 km NW Korogwe, Ambangulu Tea Estate, near Kunga village (captured by hand—FMNH 147350); 15 km NW Korogwe, near Bungo village (captured by hand—FMNH 147587, 147588).

Discussion

The Rodent Fauna of the East and West Usambara Mountains

Three years of fieldwork (1991–1993) documented 15 rodent species during relatively intensive small mammal surveys in montane portions of the East (13 species) and West Usambara Mountains (12 species). Of these 15 taxa, two (*Paraxerus vexillarius* and *Heliophobius argenteocinereus*) were only taken by hand, and the 1132 specimens collected with our standard trap and pitfall regimes represent 13 rodent species (12 in the East and 10 in the West Usambaras). All *Dendromys* specimens ($n = 11$) were obtained in pitfall devices. Most rodents collected (96.6%) during the Usambara work were taken in traps and relatively few in pitfall buckets, and as demonstrated previously at other sites in Tanzania (Stanley et al., 1996, 1998a,b), the combination of trap and bucket lines is an effective way to sample most small- to medium-sized rodents. However, larger scansorial and canopy-restricted (squirrels), and fossorial (mole rats) species were not captured with our trapping methodology.

Five species were observed on only one of the two Usambara massifs, with the genera *Aethomys* and *Paraxerus* only being collected in the West Usambara; *Dendromys*, *Rattus*, and *Graphiurus kelleni* were restricted to the East Usambara. Kingdon (1974a) stated that *P. vexillarius* is only known from the West Usambara, but recently, animals have been collected in the Nguru and Rubeho Mountains closely resembling this taxon (W. T. Stanley, unpubl. data; specimens in FMNH). Although *P. vexillarius* has not been recorded in the East Usambara Mountains, *P. palliatus* (Peters, 1852) has been observed at Amani (Swynnerton & Hayman, 1951) and Bombo Valley near the Bombo Forest Reserves (Cordeiro & Githiru, 2000). Kingdon (1974a) suggested that *P. vexillarius* might be a hybrid between *P. lucifer byatti* (Kershaw, 1923) (referred to as *P. vexillarius byatti* by Thorington & Hoffman [2005]), which is distributed on the Kilimanjaro, Usambaras, Uluguru, and Udzungwa massifs, and *P. palliatus*. Additional specimens from different localities and detailed morphological and molecular work are needed to adequately test this hypothesis. However, given phenotypically similar specimens referable to *P. vexillarius* from the West Usambara, Nguru, and Rubeho massifs, covering an expanse of approximately

TABLE 5. Abundance of rodent species in forest fragments sampled in the West Usambara based on the proportional field effort in a given forest block. Expected observations based on total number of trap-nights. Results of χ^2 tests compare expected to observed captures for each species in each fragment, and expected trap success is based on the null hypothesis of equal distribution across all fragments. Captures by techniques other than traps (i.e., pitfalls and animals brought to us by local people) are not included. Success that was greater than expected in a given fragment is shown in bold.

Species	Site (trap-nights)					Total (2810)	χ^2
	1.5 (186)	1.9 (174)	5.5 (350)	37.5 (650)	Control (1450)		
<i>Beamys hindei</i>			1			1	6.69
<i>Aethomys kaiseri</i>		1				1**	15.67**
<i>Grammomys macmillani</i>		1				1**	13.28**
<i>Grammomys ibeanus</i>	6		4	3	2	15***	32.12***
<i>Hylomyscus arcimontensis</i>			1	18	34	53**	15.96**
<i>Lophuromys aquilus</i>	3	2	2	5	2	14*	10.81*
<i>Praomys delectorum</i>	2		1	7	46	56***	24.18***
<i>Graphiurus murinus</i>				2	4	6	2.13
Total captures per site	11	4	9	35	88	147	
No. of species per site	3	2	5	5	5	9	

** P < 0.01.

*** P < 0.001.

250 km, such a large zone of introgression between these two forms seems unlikely.

Aethomys has been previously collected at 190 m near Muheza at the foot of the East Usambara (Hubbard, 1972), and excluding our exceptional West Usambara record from 1171 m and those of Makundi et al. (2006) at Magamba above 1500 m, there appear to be no records from across a broad elevational zone on these massifs. Given that dry habitat species such as *Mastomys natalensis* were found in the forests near Amani during our survey, *Aethomys* may also occur in the Amani area and was simply missed. *Rattus rattus* is a common commensal in portions of Tanzania, as previously reported from Korogwe (Swynnerton & Hayman, 1951). Hence, its occurrence in the Ambangulu area in areas of human habitation is expected. In Madagascar, *R. rattus* has colonized areas of undisturbed montane forests considerable distances from human settlements (e.g., Goodman et al., 1997; Goodman & Carleton, 1998), but after extensive rodent surveys of montane forests of Tanzania (Stanley et al., 1998b, 2000; Stanley & Hutterer, 2007; W. T. Stanley, unpubl. data), no parallel pattern was found.

Even though *Graphiurus kelleni* is considered a savannah species (Holden, 2005), this habitat characterization is too generalized based on a specimen captured within pristine forest of the EU control site, and one from the intact

Kwamgumi Forest Reserve, composed of lowland forest, at 230 m at the foot of the East Usambara (Stanley et al., 2005). *Dendromus mystacalis* is adapted to areas of cultivation (Kingdon, 1974a), and probably has a broader distribution in agricultural areas of the West Usambara than our data indicated.

Rodents in Fragments versus Control Areas

Based strictly on our trapping results (excluding *Heliophobius* and *Paraxerus*), some rodent species favored specific habitats. Examples of such preferences include *Dendromus mystacalis* in tea plantations and, with one exception, *Mastomys natalensis* and *Mus musculoides* in fallow agricultural areas. All remaining rodent species were captured in forests of different sizes (Tables 4 and 5).

Overall, the most common rodent species in the East Usambara fragments, ranked by total number of captures, are *Praomys delectorum* (56.0%); *Lophuromys aquilus* (26.7%); *Hylomyscus arcimontensis* (9.1%); and *Grammomys macmillani* (3.1%); *Beamys hindei*, *Rattus rattus*, and *Graphiurus murinus* (1.2% each); *Grammomys ibeanus* (0.9%); and *Mastomys natalensis* (0.3%). Different fragments, however, have different relative abundance rankings (Table 6). In the West Usambara, the overall ranking, based on total trap captures, was *P.*

TABLE 6. Ranking (1 = most abundant) of most common rodent species in each of the fragments surveyed in the East Usambara.

Species	Site (trap-nights)									
	0.2A (150)	0.4 (75)	0.2B (180)	0.6 (370)	0.8 (360)	3.1 (200)	2.6 (180)	3.3 (460)	29.4 (450)	Control (972)
<i>Beamys hindei</i>			3							4
<i>Grammomys macmillani</i>	1 ¹			3		3				
<i>Grammomys ibeanus</i>					2 ¹					
<i>Hylomyscus arcimontensis</i>									3 ¹	2
<i>Lophuromys aquilus</i>	1 ¹	1	1	2	1 ¹	2	1	2	2	3
<i>Mastomys natalensis</i>										6
<i>Praomys delectorum</i>			2	1	1 ¹	1	2	1	1	1
<i>Rattus rattus</i>									3 ¹	
<i>Graphiurus murinus</i>	2				2 ¹					5
No. of species	3	1	3	3	4	3	2	2	4	6

¹ Rank shared by more than one species.

TABLE 7. Ranking (1= most abundant) of most common rodent species in each of the fragments surveyed in the West Usambara.

Species	Site (trap-nights)				
	1.5 (186)	1.9 (174)	5.5 (350)	37.5 (650)	Control (1400)
<i>Beamys hindei</i>			3 ¹		
<i>Aethomys kaiseri</i>		2 ¹			
<i>Grammomys macmillani</i>		2 ¹		4	
<i>Grammomys ibeanus</i>	1		1		4 ¹
<i>Hylomyscus arcimontensis</i>			3 ¹	1	2
<i>Lophuromys aquilus</i>	2	1	2	3	4 ¹
<i>Praomys delectorum</i>	3		3 ¹	2	1
<i>Graphiurus murinus</i>				5	3
No. of species	3	3	5	5	5

¹ Rank shared by more than one species.

delectorum (38.1%); *H. arcimontensis*, (36.0%); *G. ibeanus* (10.2%); *L. aquilus* (9.5%); *Graphiurus murinus* (4.1%); and *B. hindei*, *Aethomys kaiseri*, and *Grammomys macmillani* (0.7% each). As in the East Usambara, relative abundance of each species varied among fragments (Table 7).

In general, *H. arcimontensis* and *P. delectorum* were captured in greater numbers than expected by chance (based on the assumption of equal distribution of individuals across all fragments) in the larger fragments, and both species of *Grammomys* were found in higher numbers in the smaller fragments. The capture rate of *Lophuromys* was also considerably higher in the smaller fragments and less than expected in the larger fragments in both mountain ranges.

Distribution of East and West Usambara Rodents Relative to Other Tanzanian Massifs

Three species of rodents were restricted to one of the Usambara massifs based on our trap line results: *Aethomys hindei* was trapped only in the West Usambara, and *Graphiurus kelleni* and the introduced *Rattus rattus* were only recorded from the East Usambara. All other rodent species documented during our study were found on both massifs. A finer level assessment of these taxa allow them to be divided into three groups: (1) widespread taxa that occur in disturbed open habitats, such as *Mastomys natalensis* and *Mus musculoides*; (2) species living in montane forest habitats across Tanzania regardless of the geological origin of the massif (Kilimanjaro, South Pare, West and East Usambaras, Nguu, Nguru, Ukaguru, Uluguru, Rubeho, Udzungwa, and Rungwe), such as *Grammomys ibeanus*, *Lophuromys aquilus*, and *Praomys delectorum*; and (3) species with similar distributions to group 2 and also forest dependent, but absent from younger northern volcanic mountains (Mts. Kilimanjaro and Meru), such as *Beamys hindei* and *Hylomyscus arcimontensis*. The distribution of *B. hindei* is notably broader than *H. arcimontensis*, as it also occurs in coastal forests to the east of the Usambaras (Stanley et al., 2005). Before human perturbation of natural forested habitats, the coastal formations were continuous with montane habitats of the East Usambara (Hawthorne, 1993), forming direct forested links for dispersal.

Differences between Rodent and Shrew Distributions

With few exceptions, the rodents found on the East and West Usambaras have widespread distributions across

montane habitats of Tanzania. This pattern is in contrast to that of some of the forest-dwelling shrew species found on these two massifs, particularly *Crocidura tansaniana*, *C. usambarae*, and *Sylvisorex howelli*, which have very narrow ranges and are endemics or near endemics (Stanley et al., this volume a). Hence, shrews show a greater level of local endemism, compared with rodents, in the montane forest islands of Tanzania. Current taxonomy indicates *C. monax* to have the same distribution in Tanzania as *Praomys delectorum*, from Mt. Kilimanjaro to the Southern Highlands, but we suspect detailed morphological and molecular analyses of this shrew may reveal that it encompasses more than one species.

Elevational ranges of different taxa from each small mammal group, as currently circumscribed, such as *C. monax* and *P. delectorum*, offer insights into distributional patterns, in part overlaid on vegetational formations (Lovett & Pocs, 1993). Stanley et al. (2005) found *P. delectorum*, but not *C. monax*, at 230 m in the Kwamgumi Forest Reserve, composed of lowland forest habitat (Doggart et al., 1999) at the base of the East Usambara. On the Udzungwa massif, Stanley and Hutterer (2007) surveyed across an elevational transect of 600 (lowland evergreen forest) to 2000 m (montane and mountain bamboo forest; Shangali et al., 1998) and found the lower limit of *P. delectorum* documented during that study at 600 m and *C. monax* at 1460 m (montane forest). Thus, combining this information with data from the Usambara Mountains, *C. monax* appears to be restricted to montane formations at elevations of roughly 1000 m or higher, but *Praomys* occurs notably lower in drier habitats. Today, there is no continuous topographic or montane habitat connection among the different Eastern Arc Mountains and northern volcanoes at elevations greater than 1000 m and, thus, no dispersal corridors for montane forest-restricted taxa. Moreover, the vicissitudes of Quaternary climatic change and associated vegetational shifts may have had a less dramatic effect in the formation of dispersal corridors for montane-restricted taxa such as *C. monax*, which feed largely on invertebrates (Kingdon, 1974b), compared with more generalist seed-eating mammal species, such as *P. delectorum* (Genest-Villard, 1980).

Some lower elevation habitats in southern Tanzania (Lake Masoko, 9°20'S, 33°45'E, 770 m) likely contained open wet Zambezian woodlands during the past 4000 years, with at least three episodes of habitat transformation during this period, attributed to either natural climatic change, human-induced habitat alteration, or both (Vincens et al., 2003; Ryner et al.,

2006). However, there is no evidence that *P. delectorum* uses open lowland woodland habitat either currently or historically. For example, Fernández-Jalvo et al. (1998) found evidence of woodland habitat 1.7 mya in the Olduvai Gorge, but *Praomys* was not identified from the small mammal assemblages analyzed from that period.

Although riverine forest may be a potential dispersal conduit between some massifs today, faunal surveys give no evidence that *P. delectorum* currently occurs in this habitat; hence, it does not appear to use such corridors to disperse between different massifs with montane forest. For example, this species was trapped in the South Pare at 1100 m, but not in the Gonja Forest at 500 m. The two sites are separated by approximately 8 km but, until the recent past, were connected by forest along the Higilulu River (Stanley et al., 1998a, 2000).

We hypothesize that only when the forest type currently found on the mountains of Tanzania descended to lower elevations during natural Quaternary climatic shifts could taxa such as *P. delectorum* and *C. monax* disperse among different massifs. However, given the magnitude of these vegetational shifts and very different life history strategies between these two taxa, the capacity of *Praomys* to descend to lower elevations may have allowed dispersal across lower lying topographical bridges between mountains than the more parochial *C. monax*. Given their distributions and number of specimens available, these taxa are ideal candidates for morphological and molecular genetic analyses to test these hypotheses explicitly.

Seasonal Reproduction in Montane Tanzanian Rodents

Table 8 summarizes reproductive data for three rodent species (*Lophuromys aquilus*, *Hylomyscus arcimontensis*, and *Praomys delectorum*) for numerous sites in the Eastern Arc Mountains and nearby massifs. Previous work on this topic with rodents in the Eastern Arc Mountains includes that of Makundi (1995) and Makundi et al. (2006). These widespread taxa were the most commonly captured during field inventories conducted during the dry season (July–September) and allow examination of inter-annual, inter-habitat, and inter-site variation in certain reproductive parameters.

Lophuromys aquilus is strictly terrestrial and *H. arcimontensis* is arboreal. Although *P. jacksoni* has been documented to be partially arboreal (Kingdon, 1974a), we found *P. delectorum* to be primarily terrestrial in this study (Tables 9 and 10). These life history traits influence the formulation of hypotheses regarding possible seasonal effects on variation in the position of adult male testicles being scrotal or non-scrotal. To facilitate elevational comparisons for sites on different massifs, two separate elevational zones are presented in Table 8: ≤ 1300 m and > 1300 m. We stress that the following observations are preliminary and require more study to be substantiated.

INTER-ANNUAL COMPARISONS FROM THE EAST AND WEST USAMBARAS—A comparison of the reproductive data for these three rodent species in the East Usambara indicates that the sex ratio was relatively consistent among years and species, approaching parity, except *P. delectorum* in 1992, which was notably male-biased. For species with relatively large sample sizes during a given field season, there seems to be striking difference in the proportion of males with scrotal testes. The *L. aquilus* males were notably biased toward being non-

scrotal. Very few of these non-scrotal individuals were sub-adult; hence, this skewed aspect is presumably related to seasonal reproduction. Further evidence of differences in annual reproductive seasonality can be gleaned from these data. For example, during the 1992 field season in the East Usambara, proportionately more male *H. arcimontensis* were scrotal than in *P. delectorum*, and in the former species, a greater percentage of the captured females were pregnant; this same pattern largely held for the 1993 season. The reproductive periods of these two species are apparently not synchronized.

Data on sex ratios of these rodents in the West Usambara during the three seasons shows some differences. Most notable was a female-skewed population of *H. arcimontensis* in 1992. Samples of *P. delectorum* were biased toward males in all three years, approaching and exceeding 2:1 in 1991 and 1993. Most male *H. arcimontensis* and *P. delectorum* were scrotal, but very few of the *L. aquilus* were. This is consistent with data of Makundi et al. (2006) in the Magamba Forest of the West Usambara, where seasonal variation in the latter species (noted in that paper as *L. flavopunctatus*) was found, with males being scrotal predominantly during March and April and December and January. This may imply remarkably short periods of male reproductive activity in this species and suggests an exceptional reproductive system (e.g., heavily biased polygamous reproductive strategies). For *P. delectorum* in the Magamba Forest, Makundi et al. (2006) noted that during July to September, males with abdominal testes were more common than scrotal males, but became less common between October and December. In our West Usambara samples in which $n > 4$, the number of pregnant females of these three taxa was notably low, not exceeding 9% of those examined specimens.

INTER-SITE AND INTER-HABITAT COMPARISONS FROM THE EAST AND WEST USAMBARAS—During each field season, our field inventories occurred during similar calendar periods in the East and West Usambaras; hence, the elevational range of sampled sites was a principal difference between these two massifs with regard to the reproductive condition of rodents. In the East Usambara, sites fell within the range 970 to 1150 m and, in the West Usambara, between 1170 and 1300 m (Stanley et al., this volume b). This allows for comparisons of the possible role of slight elevational differences in patterns of seasonal reproduction in these three rodent species.

For *L. aquilus*, the vast majority of males were abdominal across these two massifs and years and the sex ratio was notably close to one. Sample sizes for the percentage of pregnant females are insufficient to make meaningful comparisons. For *P. delectorum*, on both massifs, there was a greater proportion of males in the captured animals than females, and of these males, most were scrotal. Several possible explanations can be offered with regard to *P. delectorum* during the periods of our inventories: (1) males are reproductively active (with a higher proportion of scrotal testes); (2) males are defending territories (with a greater chance of being captured), although we have not found in the literature information on their reproductive ecology; and (3) males have greater home ranges, or at least are more active than females (with a greater chance of being captured). Where the data on the percentage of pregnant females in the sample are sufficient for interpretation, females in the East Usambara were more likely to be pregnant than in the West Usambara,

TABLE 8. Reproductive data for different populations of *Lophuromys*, *Hylomyscus*, and *Praomys* in the Eastern Arc Mountains and nearby massifs. All observations and measurements (in mm) were recorded between July and September, which is the dry season.

Survey	Species	Sex ratio M:F	Testes scrotal:abdominal		Testis length		Testis width		Pregnant		Largest embryo size (mm)			
			Ratio	n	Mean \pm SD	Range	n	Mean \pm SD	Range	%	n	Mean \pm SD	Range	
Mountain (m)														
Kilimanjaro (2000–4000)	<i>Lophuromys aquilus</i>	37:30		30	14.2	12–16	9.1	7–12	16	20	15	25.7 \pm 10.0	18–37	3
South Pare (1100)	<i>Praomys delectorum</i>	33:32	17:13	30	10.9 \pm 3.1	4–18	6.2 \pm 1.8	2–8	23	25	4	6		1
	<i>Hylomyscus arcinontensis</i>	0:1		35	11.2 \pm 3.4	3–15	6.3 \pm 1.8	2–8	29	0	17			
South Pare (2000)	<i>Praomys delectorum</i>	35:23	28:7	35	10	11–10	6.5	6–7	2	0	1			
	<i>Lophuromys aquilus</i>	4:1	0:4	4	12	11–13	7	7–7	2	50	4	14	12–16	2
	<i>Hylomyscus arcinontensis</i>	5:7	5:0	5	12	11–13	7	7–7	2	0	1			
Udzungwa (600–910)	<i>Praomys delectorum</i>	26:24	24:2	26	12.0 \pm 2.6	4–14	7.3 \pm 1.6	2–9	14	0	12			
	<i>Hylomyscus arcinontensis</i>	8:5	3:2	5	8.3 \pm 3.9	4–12	5.0 \pm 1.8	3–7	4	20	5	3		1
Udzungwa (1450–2000)	<i>Praomys delectorum</i>	7:7	6:1	7	12.3 \pm 0.6	12–13	7.3 \pm 0.6	7–8	3	25	4	6		1
	<i>Lophuromys aquilus</i>	34:27	1:24	25	11.5 \pm 3.0	7–15	7.0 \pm 2.2	4–10	6	0	9			
	<i>Hylomyscus arcinontensis</i>	7:9	5:1	6	10.4 \pm 2.1	7–12	6.4 \pm 1.1	5–8	5	0	6			
Ukaguru (1840–1900)	<i>Praomys delectorum</i>	26:6	25:0	25	10.9 \pm 1.2	9–14	6.9 \pm 0.8	5–8	17	13	8	2		1
	<i>Lophuromys aquilus</i>	16:24	0:7	7	12.8 \pm 1.5	11–15	8.0 \pm 0.7	7–9	5	60	5	6.8 \pm 5.2	1.5–12	3
	<i>Hylomyscus arcinontensis</i>	4:8	4:0	4	13.0 \pm 1.6	11–15	7.5 \pm 1.0	7–9	4	0	1			
Uluguru (1345–1850)	<i>Praomys delectorum</i>	23:8	23:0	23	11.7 \pm 1.6	9–14	7.1 \pm 1.2	4–9	16	0	1			
	<i>Lophuromys aquilus</i>	11:10	1:8	9	10.6 \pm 4.3	5–15	6.2 \pm 2.7	2–8	5	0	1			
Uluguru (1345–1850)	<i>Hylomyscus arcinontensis</i>	11:19	7:3	10	12.2 \pm 1.5	10–13	7.2 \pm 0.9	6–8	4	20	10	9.5	9–10	2
	<i>Praomys delectorum</i>	45:30	30:12	42	12.6 \pm 1.0	11–14	7.5 \pm 0.7	6–9	17	67	9	10.8 \pm 6.1	3–20	5
Rungwe (1870–2410)	<i>Lophuromys aquilus</i>	28:30	5:17	22	12.7 \pm 2.1	10–17	8.1 \pm 1.4	6–10	12	0	14			
	<i>Hylomyscus arcinontensis</i>	19:10	9:5	14	10.5 \pm 3.6	5–15	5.8 \pm 2.1	3–9	13	67	3	13	6–20	2
	<i>Praomys delectorum</i>	144:124	94:30	22	12.8 \pm 2.8	4–17	7.5 \pm 1.8	2–10	66	15	48	10.0 \pm 5.2	6–20	6
Nguu (1180)	<i>Lophuromys aquilus</i>	16:8	0:5	5	6.6 \pm 2.3	3–9	4.4 \pm 1.7	2–6	5	0	5			
	<i>Hylomyscus arcinontensis</i>	0:1		5										
Nguu (1430)	<i>Praomys delectorum</i>	52:37	0:5	5	12.6 \pm 1.7	8–16	7.3 \pm 1.1	4–9	27	38	13	12.6 \pm 6.5	3–21	5
	<i>Lophuromys aquilus</i>	10:7	0:10	10	11.0 \pm 1.6	9–13	7.6 \pm 1.5	6–10	5	0	0			
Nguu (1000)	<i>Hylomyscus arcinontensis</i>	1:1		7	13.3 \pm 1.2	11–15	7.4 \pm 0.5	7–8	7	80	5	10.2 \pm 8.6	2–20	4
	<i>Praomys delectorum</i>	9:8	8:0	7						0	1			
	<i>Lophuromys aquilus</i>	2:2		7										
	<i>Hylomyscus arcinontensis</i>	1:1	1:0	1	15		7		1					
Nguu (1500)	<i>Praomys delectorum</i>	18:14	14:2	16	14.1 \pm 1.1	12–15	7.1 \pm 0.3	7–8	10	0	4			
	<i>Lophuromys aquilus</i>	5:3	0:3	3	12.5	12–13	7.0	7–7	2	33	3	18		1
	<i>Hylomyscus arcinontensis</i>	0:1		11	12.6 \pm 0.5	12–13	7.4 \pm 0.5	7–8	7	0	4			
EU 1991	<i>Praomys delectorum</i>	11:6	11:0	11	13		9		1	100	1	9		1
	<i>Lophuromys aquilus</i>	5:3	1:2	3	15				1	100	1	4		1
	<i>Hylomyscus arcinontensis</i>	2:3	1:1	2					1	100	1	17.0	10–24	2
EU 1992	<i>Praomys delectorum</i>	3:2	3:0	3	9.3 \pm 2.4	3–13	6.0 \pm 1.5	2–8	19	18	17	31	30–32	2
	<i>Lophuromys aquilus</i>	50:43	23:24	47	12.1 \pm 4.6	3–17	6.3 \pm 2.1	2–9	14	25	8	5	4–6	2
	<i>Hylomyscus arcinontensis</i>	18:13	13:3	16	10.2 \pm 3.7	3–15	5.6 \pm 2.1	1–9	61	14	42	11.7 \pm 6.2	6–22	6
	<i>Praomys delectorum</i>	106:79	64:33	97	9.8 \pm 1.8	7–11	6.6 \pm 1.1	5–8	5	33	3	30		1
EU 1993	<i>Lophuromys aquilus</i>	10:8	1:9	10	14 \pm 1.0	13–15	6.7 \pm 0.6	6–7	3	50	4	4	3–5	2
	<i>Hylomyscus arcinontensis</i>	3:6	3:0	3	12.7 \pm 1.6	11–17	6.3 \pm 1.5	3–8	15	8	12	11		1
	<i>Praomys delectorum</i>	30:24	22:5	27	8.2 \pm 2.9	6–13	4.8 \pm 1.3	4–7	5	0	3			
WU 1991	<i>Lophuromys aquilus</i>	21:19	4:13	17	13.0 \pm 2.7	7–17	6.5 \pm 1.8	3–10	26	0	13			
	<i>Hylomyscus arcinontensis</i>	51:42	48:1	49	12.0 \pm 2.9	5–17	6.1 \pm 1.6	2–8	15	0	7			
	<i>Praomys delectorum</i>	51:23	37:12	49										

TABLE 8. Continued.

Survey	Species	Sex ratio		Testes scrotal:abdominal		Testis length		Testis width		Pregnant		Largest embryo size (mm)	
		M:F	Ratio	n	Mean \pm SD	Range	n	Mean \pm SD	Range	%	n	Mean \pm SD	Range
WU 1992	<i>Lophuromys aquilus</i>	4:4	2:2	4	11.5 \pm 3.5	9-14	2	6.5 \pm 0.7	6-7	2	50	3	1
	<i>Hylomyscus arcimontensis</i>	15:29	14:0	14	13.6 \pm 1.9	11-17	8	7.2 \pm 1.2	6-9	8	0	15	1
	<i>Praomys delectorum</i>	32:24	29:2	31	13.7 \pm 1.8	11-17	16	7.1 \pm 1.0	6-9	16	9	5	1
WU 1993	<i>Lophuromys aquilus</i>	1:1	0:1	1			2	7.5	7-8	2	100	8	1
	<i>Hylomyscus arcimontensis</i>	4:1	4:0	4	12.5	11-14	2	6.6 \pm 2.1	3-8	5			
	<i>Praomys delectorum</i>	13:4	11:1	12	11.0 \pm 3.3	6-14	5						

which might relate to elevation and seasonality of reproduction. In general, the same general patterns between the two massifs can be gleaned for *H. arcimontensis*. Most striking in this regard is the percentage of pregnant females between the two massifs. In 1992 and 1993 in the East Usambara, 25% (n = 8) and 50% (n = 4) of the females were pregnant; in 1992, 0% of 15 females were pregnant in the West Usambara.

INTER-HABITAT COMPARISONS FROM THE SOUTH PARE—The important elevational difference between the two South Pare sites, 1100 (surveyed in July 1993) and 2000 m (surveyed in August 1994; Stanley et al., 1996, 1998), also allow for consideration of the potential effect of elevation in reproductive seasonality. Comparable data and sample sizes from the two South Pare sites are only available for *P. delectorum*. At both 1100 and 2000 m, the sex ratio in this rodent was close to parity, but captured males were disproportionately skewed toward those with scrotal testes. Even though numerous females were dissected from these two elevational zones, no females were found with embryos. Hence, at this level of comparison, for two sites in montane forest separated by 900 m elevation, no important difference was found in aspects of reproduction in *P. delectorum*.

INTER-HABITAT COMPARISONS FROM UZUNGWA—Lowland rainforest between 600 and 910 m and sub-montane forest to mountain bamboo forest between 1450 and 2000 m (Stanley & Hutterer, 2007) were surveyed between July and September 1995 in the Uzungwa. The ecological contrasts at these sites are notably more pronounced than those of the East and West Usambaras and the South Pare. Data are available from this massif for two taxa, *P. delectorum* and *H. arcimontensis*, but sample sizes in a few cases are not substantial.

Sex ratios at the lower sites approached one; at the higher zone, male *P. delectorum* were disproportionately represented. Consistent with other sites in the Eastern Arc and nearby mountains, (1) most males captured for both species were scrotal, particularly in *P. delectorum*, and (2) more females were pregnant in the lower elevational zone. This suggests that the reproductive season commences earlier or has a broader period in the lowland rainforest compared with the higher formations.

Rodent Species Previously Reported in the East and West Usambaras and Not Documented during This Study

Several rodent taxa that had been previously reported from the Usambara Mountains were not found in our 1991–1993 field studies, likely due to trapping methodologies. *Otomys sungae* Bohmann, 1943, has been collected in the West Usambara in the Magamba Forest at 1585 m (Musser & Carleton, 2005; specimens in FMNH). As a strict herbivore, *Otomys* is not commonly attracted to our traps baited with coconut and peanut butter. However, *O. sungae* may occur in an elevational zone higher than that we sampled, which was below 1300 m.

Makundi et al. (2003) collected *Arvicanthis nairobe* J. A. Allen, 1909 from Shume Ward (4°42'16"S, 38°12'16"E, above 1800 m) in the West Usambara. This species was captured in traps baited with peanut butter mixed with maize bran in both fallow land and forest. Although the absence of this species from our study sites may be associated with a higher elevational range than that of our study, it occurs in dry habitats at approximately 1000 m in Tarangire National Park

TABLE 9. Microhabitat occurrences of rodent species by fragment size in the East Usambara Mountain in 1992. Data for the control area come from trap lines AF, AG, and AI only (Stanley et al., this volume a). Explanations for information on trap placements are keyed to numerical notes presented at foot of table.

Fragment size and rodent species	No. trapped	Trap position										
		Above ground			Ground location ¹					Above ground location ²		
		On ground	≤1 m above ground	>1 m above ground	Leaf litter, 1	Herbaceous vegetation, near rotten wood, 2	Under or near (<30 cm away) highly decomposed logs or stumps, 3	By roots, trunks, and logs, 4	Misc., 5	Vine, limb or trunk <10 cm, 6	Vine, limb or trunk >10 cm, 7	Misc., 8
1–10 ha												
Trap distribution		240	48	83	19	35	34	75	77	81	7	43
<i>Beamys</i>	1			1								1
<i>Lophuromys</i>	33	32	1			8	3	14	7	1		
<i>Grammomys ibeanus</i>	1		1									1
<i>Grammomys macmillani</i>	10	6	1	3		1		3	2	2		2
<i>Praomys</i>	40	38	2		1	3	3	10	21	2		
29.4 ha												
Trap distribution		70	8	12	14		19	25	12	15	1	4
<i>Lophuromys</i>	5	5					2	3				
<i>Hylomyscus</i>	1			1						1		
<i>Praomys</i>	13	12	1		6		1	1	4	1		
<i>Rattus</i>	1	1							1			
Control												
Trap distribution		154	28	42	22	6	30	58	38	49	6	15
<i>Beamys</i>	3	2		1				2		1		
<i>Lophuromys</i>	5	5					1	2	3			
<i>Hylomyscus</i>	16	10	2	4	1			5	4	4	1	1
<i>Mastomys</i>	1	1							1			
<i>Praomys</i>	44	37	5	2	3	3	15	6	10	3	1	3
<i>Graphiurus</i>	2	2						2				

¹ **On ground:** (1) In area of open understory; (2) in thick herbaceous vegetation; (3) under or near (<30 cm away) highly decomposed logs or stumps; (4) under or near living or recently fallen tree parts, including roots, trunks, and logs; (5) miscellaneous, including on muddy stream banks and in, under, or near (<30 cm away) large rocks or rock piles (both exposed or covered with moss).

² **Above ground:** (6) On vines, limbs, or trunks less than 10 cm in diameter regardless of orientation; (7) on limbs or trunks greater than 10 cm in diameter; (8) miscellaneous settings.

(Stanley et al., 2007c), and may have recently colonized the Shume area.

Acomys ignitus Dollman, 1910, has been noted in the literature as occurring in the “Usambara Mountains” (e.g., Musser & Carleton, 2005), and this species has been referred to as a “near endemic” to the Usambara massifs (Burgess et al., 1998). The type locality of *A. ignitus* is Voi, Kenya, but little is known about its distributional range. J. T. Zimmer collected two specimens referable to this species in 1926. The first (FMNH 27295) was obtained near Lake Manka at approximately 435 m. Other mammals from the same collection and locality include the gazelle *Litocranius walleri*, a distinctly dry habitat animal. The second *A. ignitus* (FMNH 27296) was collected near Mnazi, at approximately 600 m and adjacent to drier habitats. Both sites are lowland dry habitats, and it is inappropriate for *A. ignitus* to be listed among the montane mammals of the Usambaras or to be considered endemic or near-endemic to these massifs.

Cricetomys ansorgei Thomas, 1904, was documented by Cordeiro et al. (2009; as *C. gambianus* Waterhouse, 1840) in the forests of the Amani area, and we found traps set by local residents for this large rodent in the West Usambara 37.8-ha fragment. Although *Rattus rattus* was found during our study, other commensals, such as *Mus musculus* Linnaeus, 1758, were

not. Given that most of our trapping was away from human habitation, it is not surprising that these two species were rare or absent in our captures.

Conclusions

The rodent fauna of the East and West Usambara Mountains is diverse and remains poorly studied. In particular, we know little about historical shifts in rodent species and elevational distribution as a function of human-induced habitat alteration. This has important bearing, for example, associated with the range of *Mastomys* and its ectoparasites, which are reservoirs of bubonic plague in the West Usambara (Kilonzo et al., 1997). Furthermore, certain rodent species are presumed to be important dispersers of seeds and fruits. Hence, they likely play an important role in tree regeneration and, by extrapolation, the integrity of the forest ecosystem. Additional field surveys and associated morphological and molecular genetic analyses are needed to place the rodent fauna of the Usambara massifs in a broader perspective with regards to other mountain complexes in the eastern portion of Africa and should provide further insight into the reproductive systems and aspects of seasonality in these animals.

TABLE 10. Microhabitat occurrences of rodent species by fragment size in the West Usambara Mountains in 1991. Data for the control area come from trap lines A and B only (see Stanley et al., this volume a). Explanations for information on trap placements are keyed to numerical notes presented at foot of table.

Fragment size and species	No. taken	Trap position										
		Above ground			Ground location ¹				Above ground location ²			
		On Ground	≤1 m above ground, A	>1 m above ground, B	Leaf litter, 1	Herbaceous vegetation, 2	Under or near rotten wood, 3	By roots, trunks, fresh logs, 4	Misc., 5	Vine, limb, or trunk <10 cm, 6	Vine, limb, or trunk >10 cm, 7	Misc., 8
1–10 ha												
Trap distribution		65	19	26	21	17	8	13	6	28	13	4
<i>Aethomys</i>	1	1			1							
<i>Beamys</i>	1	1				1						
<i>Lophuromys</i>	7	7				5	1		1			
<i>Grammomys ibeanus</i>	10		1	9						8	2	
<i>Grammomys macmillani</i>	1		1							1		
<i>Hylomyscus</i>	1			1						1		
<i>Praomys</i>	3	3			1		2					
37.8 ha												
Trap distribution		66	20	14	3	7	10	22	24	17	11	6
<i>Lophuromys</i>	5	5				4			1			
<i>Grammomys ibeanus</i>	3		3						3			
<i>Hylomyscus</i>	18	8	3	7		2		2	4	8	2	
<i>Praomys</i>	7	7				1	1	1	4			
<i>Graphiurus</i>	2	1	1						1		1	
Control												
Trap distribution		150	22	28	6	3	34	56	51	26	17	7
<i>Lophuromys</i>	2	2			1			1				
<i>Grammomys ibeanus</i>	2	2			1		1					
<i>Hylomyscus</i>	34	12	5	17	1		1	4	6	13	3	6
<i>Praomys</i>	46	36	6	4	2		11	11	12	4	4	2
<i>Graphiurus</i>	4	2	1	1				2		1	1	

¹ **On ground:** (1) In area of open understory; (2) in thick herbaceous vegetation; (3) under or near (<30 cm away) highly decomposed logs or stumps; (4) under or near living or recently fallen tree parts, including roots, trunks, and logs; (5) miscellaneous, including on muddy stream banks and in, under, or near (<30 cm away) large rocks or rock piles (both exposed or covered with moss).

² **Above ground:** (6) On vines, limbs, or trunks less than 10 cm in diameter regardless of orientation; (7) on limbs or trunks greater than 10 cm in diameter; (8) miscellaneous settings.

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