

Ecology of rodent communities in agricultural habitats in eastern Sierra Leone: Cocoa groves as forest refugia

ADRIAN ASHTON BARNETT,¹ NICHOLAS READ,² JONATHAN SCURLOCK,³
CHRISTOPHER LOW,⁴ HUGH NORRIS⁵ & REBECCA SHAPLEY⁶

¹*School of Life Sciences, University of Surrey Roehampton, West Hill, London SW15 3SN, England;* ²*The Vicarage, Lydbury North, Shropshire, SY 78AU, England;* ³*Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Bldg 1507, MS 6407, Bethel Valley Road, Oak Ridge, TN 37831-6407, USA;* ⁴*c/o St. Peter's College, Oxford, England,* ⁵*c/o Keble College, Oxford, England;* ⁶*Akodon Ecological Consulting, 20 Cora Court, Walnut Creek, CA 94596, USA*

Abstract: Ten species of rodents were trapped from cocoa groves, abandoned agricultural land and a rice field during the wet season in eastern Sierra Leone. Trap success varied between 0.8% and 14.1%. Mean corrected trap success was 6.4%. Data are analyzed in terms of habitat preferences of individual species, community composition and species richness. Results of dietary analysis are presented. The data indicate that the rodent fauna of cocoa groves contains both savanna-derived and forest-derived elements, though some habitat specialist species were absent. Habitats with a high percentage of understory cover showed a higher rodent species diversity and biomass than those with a sparse understory. The habitats contained 43% of the predicted small mammal fauna, including 33% of the forest-dwelling species. Missing species were mostly arboreal forms. Cocoa groves may provide important refugia for forest-derived small mammal species in areas where deforestation has been extensive.

Resumen: Fueron atrapadas diez especies de roedores en cacaotales, campos agrícolas abandonados y un cultivo de arroz durante la estación húmeda en el este de Sierra Leona. El éxito del trampeo varió entre 0.9% y 14.2%. El éxito promedio corregido de trampeo fue 6.5%. Los datos fueron analizados en términos de preferencias de hábitat de las especies individuales, la composición de la comunidad y la riqueza de especies. Se presentan resultados del análisis de las dietas. Los datos indican que la fauna de roedores de los cacaotales contiene elementos derivados tanto de la sabana como del bosque, si bien algunos especialistas estuvieron ausentes. Los hábitats contuvieron 43% de la fauna de mamíferos pequeños, incluyendo un 33% de especies que habitan el bosque. Las especies ausentes correspondieron mayormente a formas arbóreas. Los cacaotales pueden representar importantes refugios para las especies de mamíferos pequeños procedentes del bosque en áreas extensamente deforestadas.

Resumo: Dez tipos de roedores foram capturados em cacauais, terras agrícolas abandonadas e arrozais durante a estação húmida na zona oriental da Serra Leoa. O sucesso das capturas variou entre os 0,8% e os 14,1%. A média corrigida do sucesso das capturas foi de 6,4%. Os dados foram analisados em termos das preferências de habitat pelas espécies individuais, composição da comunidade e riqueza específica. Os resultados da análise das dietas são igualmente apresentados. Os dados indicam que a fauna de roedores dos cacauais contem quer os elementos que habitam a savana quer os da floresta, se bem que as espécies com habitats especializados estejam ausentes. Habitats com uma elevada cobertura de sub-bosque mostraram a

a existência de uma mais alta diversidade de espécies de roedores e de biomassa do que aqueles com um sub-bosque exparso. Os habitats continham 43% da fauna predita de pequenos mamíferos, incluindo 33% da fauna presente na floresta. A maior parte das espécies não representadas eram maioritariamente as do estrato arbóreo. Os cacauis podem proporcionar um refúgio importante para os pequenos mamíferos de habitat florestal naquelas áreas onde a desflorestação tem sido extensiva.

Key words: Cocoa, deforestation, diversity, rainforest, refugia, rodents, Sierra Leone, vegetation density.

Introduction

Studies of rodent ecology in Africa have been reviewed by Delany (1972, 1986) and by Fleming (1975). The majority of published surveys on small mammals are from East and Central Africa.¹ Of the countries lying within the Upper Guinea Forest Block (*sensu* Sayer *et al.* 1992), Sierra Leone is probably the least well studied in terms of rodent ecology.² With a few exceptions (Carleton & Robbins 1985; Cross 1977; Jaeger *et al.* 1966; Jones 1966; Taylor 1984), research has concentrated on either the economic impact of rodents (*e.g.* Taylor 1961), or on their disease carrying capabilities (*e.g.* Demartini *et al.* 1975; French 1979, 1985; Keenlyside *et al.* 1983; Monath *et al.* 1974). More recent surveys deal only with larger mammals (*e.g.* Ausden & Wood 1990), or contain only non-quantitative information on small mammals (Broad & Turner 1992). This paper results from a survey in eastern Sierra Leone between July and September, 1980, which compared the rodent fauna of cocoa groves of different ages with those of other habitats exhibiting different degrees of canopy development and different types of agricultural management. Deforestation in the general region has been extensive (Barnes 1990) and local extinctions of forest taxa have been widespread (Barnett & Prangley 1997; Decher 1997; Happold 1973, 1994; Struhsaker & Oates 1995). To test the value of cocoa groves as refugia for forest-derived rodents, comparisons are also made between the rodent community of the cocoa groves and those reported from surviving primary for-

ests in Sierra Leone and elsewhere in the West African forest block.

Study area

Fieldwork was conducted around Saama, a small village (approximate population, 200) in the Lower Bambara Chiefdom, Eastern Province, Sierra Leone (Fig. 1). The village (170 m a.m.s.l.) did not appear on any published maps known to us, but is approximately 65 kilometers northeast of the capital of the Province, Kenema (grid ref. 07°48' N, 11°04' W) and lies in the upper Moa River basin. According to Clarke (1966) and Cross (1977), the average annual rainfall for this region is between 2500 mm and 3050 mm, most falling between May and December.

Agriculture was typical for this region (Mitchell 1989; Paxton 1990), consisting of subsistence cultivation of rice, intercropped with maize, yams, okra, pumpkins and groundnuts. Cocoa (*Theobroma cacao*: Sturculiaceae) provided the main cash crop, though citrus, coffee, oil palm, banana and pineapple were also grown in plantations of 2 to 25 ha. As is common in West Africa (Amoah *et al.* 1995; Ekanade 1998), oil palms provided an emergent shading overstory in the cocoa groves. The upper Moa River basin is on the border between two vegetation types: "lowland and secondary grassland mosaic" and "Guineo-Congolian lowland rainforest" (White 1983). Little natural forest survives locally (Harcourt 1992), apart from that at the nearby Gola Forest Reserve (see Allport *et al.* 1989).

¹ From 1968-1999 Zoological Record records the following papers published on native, wild-living, non-volant mammals (sm. mammals/lg. mammals): Kenya 121/892; Tanzania 57/790; Uganda 27/379; Zaire 26/325.

² From 1968-1999 Zoological Record records the following papers published on native, wild-living, non-volant mammals (sm. mammals/lg. mammals): Guinea; 24/33; Sierra Leone 13/63; Ivory Coast 48/137; Ghana 19/45.

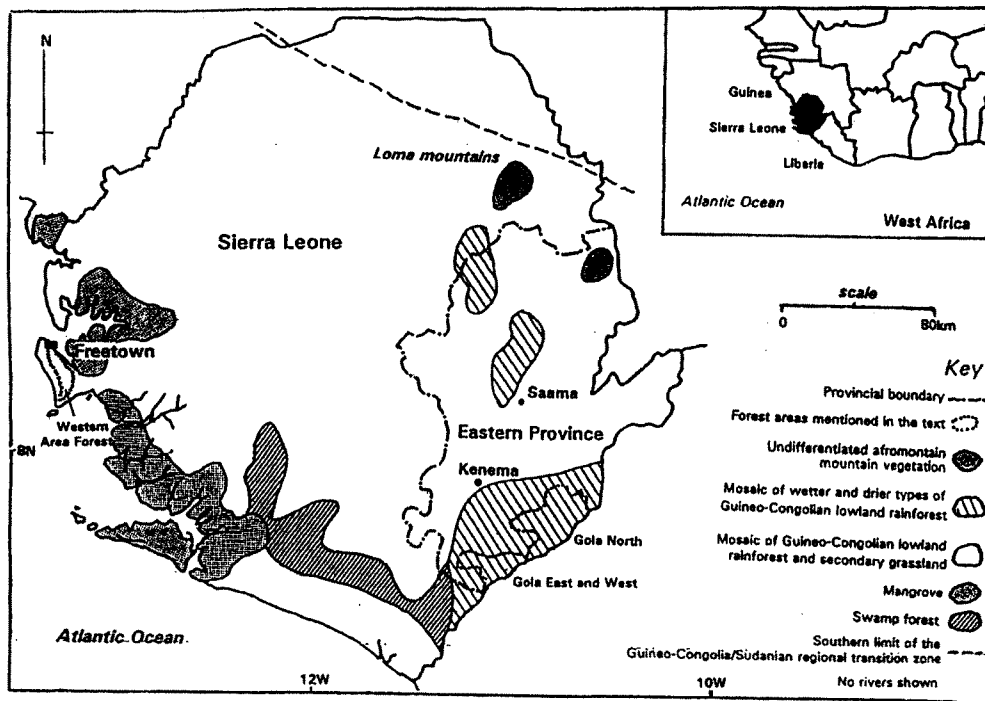


Fig. 1. Map of Sierra Leone showing the forest areas mentioned in the text.

Methods

Trapping was conducted in four actively managed cocoa groves. Each grove was an irregular polygon between three and eight ha in extent. Two contained three-year-old plants of *Theobroma cacao* and one each had 10- and 40-year-old *T. cacao*. Additional trapping was conducted in formerly-cropped fields now dominated by elephant grass (*Pennisetum purpureum*: Poaceae), and in a rice field cleared five months previously from secondary forest. In one three-year-old cocoa grove all groundcover had recently been manually removed with bush knives ('brushed'). Fieldwork was conducted between July and September, 1980, during the wet season for the region.

In each cocoa grove one 50 m x 50 m sampling grid was set up as near as possible to the grove's centre. To maximize trapped sample representativeness (see Neal & Cock 1969), both small and large snap-traps were used. The ratio of small to large traps was 1:2. To maximize capture rates over the sampling period (Barnett & Dutton 1995), traps were deployed at high density within the sampling grids. Within each 50 m x 50 m grid traps were positioned at sites of rodent activity (holes, runs, logs etc. - see Barnett & Dutton 1995),

with four traps situated within 3 m of each 10 m marker stake. A further trap was positioned approximately mid-way between each 10 m marker. Of this total of 204 traps, four of these were placed arboreally. A further 46 traps were positioned at suitable arboreal locations throughout the grid, bringing the total of traps placed on the trunks and limbs of trees to 20% (50 of 250). On grid two an additional 41 trap nights were added to areas central to selected grid quadrants. To maintain comparability, this practice was also used on all subsequent trapping grids.

Terrestrial traps were tied to stakes to reduce trap loss to small carnivores (see Barnett & Dutton 1995). Arboreal traps were lashed to trees at a position within 2 m of the ground. All traps were flagged with 'Fabglo' hazard warning tape (JPS Ltd., Minster Lovell, Oxford OX8 5RX, UK), to aid trap retrieval and reduce vegetation trampling. After the first grove the use of wooden traps was discontinued as they became swollen in wet conditions and the treadles ceased to function reliably. Metal snap-traps (Self-set Co., Falcon Works, Middlesex TW16 5DE, UK) were used at all subsequent sites. Traps were baited, but not set, for one night, then baited, set and run for four consecutive days and nights. Bait, a paste of rolled oats, pea-

nut butter, bananas and vegetable oil, was applied each day at dusk. Traps were checked daily at 0700, 1200 and 1700. The number of trap nights per site is given in Table 1. The same baiting format was used at the six stations set in a single pathway cut through the head-high *Pennisetum* grass. Trapping stations were 10 m apart, each with two large Havahart live traps (positioned back-to-back) and two snap traps. In the rice field two 50 m transects were laid at right angles, with a two-trap trapping station every 5 m and baited as above. In addition, four large Havahart live traps, baited with cassava were placed in the runs of *Thryonomys swinderianus* (Temminck 1827).

Each captured animal was weighed to the nearest 0.5 g and lengths of head/body, tail, hind foot (s.u.) and ear measured to the nearest mm. Ants sometimes partially ate carcasses before they were retrieved. In such cases the affected parts were not measured. Captures were identified in the field using keys in Delan (1975), Kingdon (1974) and Rosevear (1969). Identifications were later checked against specimens in the collection of the Natural History Museum, London. Nomenclature in this paper follows Wilson & Reeder (1993). A representative collection of skins and skulls was prepared following Corbet (1968) and deposited at the Natural History Museum, London. Sex and reproductive condition were recorded. Males were classified as scrotal (breeding) or abdominal (non-breeding) according to testes position. Females were recorded as pregnant, lactating (judged by the presence of nipple halos and/or exuding milk) or non-breeding.

Diet was investigated by microscopic analysis of stomach contents. Stomachs were removed during routine dissection and, following Cole (1975),

were stored in Formyl Acetic Acid. Analysis followed Cole (1975): stomach contents were spread onto a Petri dish, dried and, under a dissecting microscope, sorted into categories; material in each category was then spread on a Petri dish backed with a 1 x 1 mm grid and the absolute area covered was calculated. This was then summed and converted to a percentage for each stomach. Food items were categorized as leaf, stem, palm nut flesh, fibre, seed, invertebrate. Following Churchfield (1985), results were expressed as the mean percentage of the relative volume of a food item in the stomach (the per species mean of each food item for the total number of individuals in that species that analysis revealed to have eaten items in that category).

Maps of vegetation cover were made in cocoa groves for each 10 m x 10 m square of the 50 m x 50 m trapping grids. For this purpose, each 10 m x 10 m square was divided with markers into 1 m x 1 m subplots. Plant cover was allocated to four categories: leaf litter, vegetation up to 25 cm tall, from 25.1 cm to 75 cm tall, and taller than 75 cm. Vegetation height was measured at each 1 m marker. Categories reflecting the percentage of vegetation cover were assigned to each 1 m x 1 m subplot. The values for each sub-plot were visually estimated and were based on the proportion of ground in each sub-plot that was obscured from view by vegetation when seen from directly above. Categories were: sparse cover, 0-30% of the ground obscured; medium cover, 31-60% of the ground obscured; dense cover, 61% + of the ground obscured). This procedure was conducted for each subplot and then summed for each 10 m x 10 m square and then repeated until the whole grove was mapped. The positions of cocoa and shade

Table 1. Trapping results for each site.

	Site					
	1	2	3	4	5	6
No. trap nights	1000	1041	1041	1041	72	120
No. captures	22	22	7	64	6	17
Trap success (%)	2.2	2.11	0.67	6.14	8.33	14.16
No. sprung traps	85	108	124	206	0	0
Sprung traps (%)	8.5	10.3	11.9	19.7	-	-
Corrected trap success	2.65	2.66	0.88	10.17	8.33	14.16

Corrected Trap Success was calculated using the corrected percentage trap success ratio of Ruffer (1961). For non-target taxa, traps were sprung by (in order of importance): ants, wind and rain, West African giant snails (*Achatina achatina*), falling debris and frogs; Sites: 1 = ten-year-old cocoa grove (sparse undergrowth); 2 = forty-year-old cocoa grove (moderate undergrowth); 3 = 3-year-old cocoa grove (undergrowth removed); 4 = 3-year-old cocoa grove (dense undergrowth); 5 = elephant grass field; and 6 = rice field.

trees and fallen logs within each 10 m x 10 m square were also plotted and added to the map of vegetation distribution. To minimize disturbance this was conducted the day after trapping had finished. No mapping was undertaken in the other study habitats.³

Results

Trapping

A total of 138 animals of 10 species were caught over six sites in 4315 trap nights (all trap types combined), representing a mean trap success of 3.19%. Five hundred and twenty three traps were sprung by non-target events (12.12%). Using

the corrected percentage trap success ratio of Ruffer (1961) to compensate for this, the corrected trap success is 6.47%. Thirty-four (25%) specimens were damaged or destroyed by foraging ants, and five were damaged by other scavengers. Most animals were active at night; only three animals (all *Mus* [*Nannomys*] sp [p.]) were picked-up from mid-day trap checks and two (one *Mus* [*Nannomys*] sp [p.] and one *Lophuromys*) at dusk.

Table 1 gives trapping results per trapping site. For each trapping site Table 2 gives the relative abundance and reproductive demography of small mammal species recorded. Calculations of species richness, a diversity index (MacArthur 1972), a corrected trap success index (Ruffer 1961) and trap catch biomass are given in Table 3.

Table 2. Reproductive demography and distributions of trapped small mammals.

Demography						Species	Sites						Total
MM	P/LF	MF	IM	IF	U		1	2	3	4	5	6	
				1		<i>Cricetomys emini</i>				1			1
1						<i>Hybomys trivirgatus</i>				1			1
2				2		<i>Hylomyscus alleni</i>	1	1		2			4
1						<i>Lemniscomys striatus</i>							1
5	3	1		1		<i>Lophuromys sikapusi</i>	1	2		2	4	1	10
3		1	3	1		<i>Mastomys erythroleucus</i>	1	1		1	1	4	8
31	8	3	19	11	11	<i>Mus</i> sp.(p.)	18	10	6	40		9	83
11	5	3	4	4		<i>Praomys tullbergi</i>		7	1	17		2	27
						<i>Rattus rattus</i>	1						1
	1					<i>Uranomys ruddi</i>					1		1
1						Unidentified		1					1
55	17	8	26	20	12	Totals	22	22	7	64	6	17	138

Also, four *R. rattus* and two *Mus* sp.(p.) were trapped in camp. Code: MM = mature male; P/LF = pregnant or lactating female; MF = mature female (non-reproductive); IM = immature male; IF = immature female; U = undetermined due to ant damage.

Table 3. Species richness and diversity for each site.

	Site					
	1	2	3	4	5	6
Species richness	5	6	2	7	3	5
Diversity index	1.48	2.85	1.32	2.2	2.0	2.27
Corrected index	0.3	0.48	0.66	0.31	0.67	0.57
Trap biomass	45.9	54.9	8.4	207.1	542.5	556.2

Species richness = the number of species trapped per site. Diversity index was calculated following MacArthur (1972). A corrected index (diversity index/species richness) allows comparisons to be made between habitats. Trap biomass was calculated as the average collective weight (g) of rodents caught per 100 trap nights.

³ A plant species list can be obtained from JS. This shows the botanical composition of the study site closely resembled those of Clayton (1958) and Komolafe (1977), authors who provide a detailed botanical description of cocoa grove understory vegetation.

Diet

Dietary information was obtained for 56 specimens from seven species. These data are presented in Table 4. Considerable quantities of hair were observed in several stomachs but, as this was always the same colour and length as the pelage of the specimen and was not accompanied by bone, this was taken as evidence of grooming rather than carnivory or cannibalism.

Reproduction

Reproductive activity was recorded for 126 animals (see Table 2). Twelve animals were damaged by ants and could not be sexed.

Association of rodents with vegetation cover classes

Data from vegetation mapping are summarized in Table 5. Forty-six (40%) of the 115 animals caught in cocoa groves were caught in portions of the grove assigned to the 'dense cover' category, 49 individuals (43%) were trapped in vegetation with medium cover and 20 (17%) in areas where the vegetation had been assigned to the 'sparse cover' category.

Other mammal species seen (but not trapped) during the study are given in Appendix I.

Species accounts

Cricetomys emini (Wroughton 1910)

A single specimen, a juvenile female, was taken in the dense vegetation of a 3-year-old cocoa grove. According to Happold (1987, p. 124), *C. emini* occurs only in undisturbed rainforest and is not associated with farmlands. Yet misidentification of *C. emini* is unlikely as the species is easily distinguished in the hand from *C. gambianus* Waterhouse, 1840 (see Rosevear 1969; Happold 1987). Measurements in Rosevear (1969) indicate that the captured individual was about 76% of average adult size. Presence in an agricultural habitat may, therefore, be the result of pre-pubescent dispersal.

Hybomys trivirgatus (Temminck 1853)

This species was trapped in thick underbrush near a stream in the centre of a three-year-old cocoa grove. Cole (1975) and Carleton & Robbins (1985) report *Hybomys* to prefer dense moist vegetation. From distribution maps in Carleton & Robbins (1985), this specimen of *H. trivirgatus* is at the extreme western edge of the species' range (but see Grubb *et al.* 1998).

Hylomyscus alleni (Waterhouse 1838)

Five specimens were caught, all in parts of the cocoa groves classified as 'dense cover'. Two were

Table 4. Results of diet analysis for six rodent species.

	Hylomyscus (N=4)		Hybomys (N=1)		Lemniscomys (N=1)		Mus sp.(p.) (N=24)		Praomys (N=18)		Lophuromys (N=7)	
	n	% vol	n	% vol	n	% vol	n	% vol	n	% vol	n	% vol
Leaf							19	54.7	14	52.2		
Stem							19	14.0	8	19.7		
Oil palm pulp	4	70.3	1	7.0			3	4.4	8	19.2		
Fibre		80.0	1	11.5			10	9.6	9	10.7	4	20
Seed	1	28.5	1	21.5	1	100					2	+
Invertebrate	1	17.5	1	60.0			2	9.6	4	9.6	7	48
Coleoptera:ad	1										2	+
Coleoptera:lar							1	6.0	2	5.0	1	+
Formicidae			1	30.0							7	46.7
Lepidoptera:Lar	1	11.0									1	+
Diplopoda												
Arachnida			1	30.0			1	3.6	2	4.6		
Oligochaeta											2	67.5
Mollusca											1	+

Numbers of stomachs analyzed per species given in parentheses; n = number of stomachs containing item, % vol = mean % of relative volume; + = trace present, ad = adult, lar = larvae.

Table 5. Cocoa grove understory vegetation cover.

Grove No.	Age (yrs)	Understory cover (percentage of the understory of each grove's study grid in each of the following categories)				Classification
		None	Low	Medium	High*	
1	10	12	84	4		sparse
2	40			32	68	moderate
3	3			12	88	dense
4	3	92	8			recently cleared

* low = 1-30%, medium = 31-60%, high 61%+ (see methods section for further details)

at the periphery of the grids, two and three in the centre. Three were trapped within 1 m of the ground and two were caught in terrestrial traps. Though some workers (e.g. Isabajye-Basuta & Kasenene 1987) found *Hylomyscus* in lower numbers in degraded forest than in disturbed forest, it appears that the preferred habitat of this species is provided by shrubs and tangles in secondary forest and abandoned farmlands within the rainforest zone (Grubb *et al.* 1998; Happold 1977, 1987; Kingdon 1997). In Ghana, Jeffrey (1977) found *Hylomyscus* to occur at low densities in habitat types with dense vegetation. Grubb *et al.* (1998) report similar habitat preferences in Sierra Leone.

Lemniscomys striatus (Linn. 1758)

According to Happold (1987), *L. striatus* prefers grasslands with dense undergrowth, especially those near swamps. We captured a single specimen, in a fallow non-irrigated rice field free of underbrush but near a marshy area. As in the current study, Jeffrey (1977) found *Lemniscomys striatus* to be absent from forested habitats, being present in fields and commonest in deserted arable land (where it dominated).

Lophuromys sikapusi (Temminck 1853)

Lophuromys sikapusi was found in all trapped habitats except recently brushed cocoa grove, with the greatest number in *Pennisetum* grassland. All specimens were taken in dense vegetation. A preference for dense vegetation is corroborated by Jeffrey (1973), who failed to trap this species in mature cocoa groves where dense canopy inhibited undergrowth development. In Ghana, Jeffrey (1977) found *L. sikapusi* to be most abundant in

deserted arable land. Grubb *et al.* (1998) report similar circumstances in Sierra Leone.

Mastomys erythroleucus (Temminck 1853)⁴

Members of this genus occur in natural clearings and man-made habitats and avoid closed habitats (Happold 1987). The seven specimens caught in the current study also demonstrated these preferences. Though three were caught well within cocoa groves, the traps were located in sparse vegetation. This species has considerable powers of dispersal and can move easily though non-optimal habitats (Jeffrey 1977), and it is notable that all three animals from cocoa groves were immature. Four reproductively active adults were caught in open grassy habitats, a more standard habitat for the genus. Interestingly, Jeffrey (1973) reports that *Mastomys* cannot coexist with *Rattus rattus*. This was borne out in the present study. Despite its known facility for commensalism (Lapshov & Inapogui 1993; Ter-Muelen *et al.* 1996), *M. erythroleucus* occurred in fields, while *R. rattus* was largely confined to human habitation. Brambell & Davis (1941) reported weight at puberty for *Mastomys* to be 40 g. Non-reproducing females exceeding this weight were taken in the current study. This may reflect a more strongly marked breeding season of *Mastomys*, the result of a greater seasonal fluctuation in available food (Cross 1977; Delany 1986) in non-forest habitats.

Mus (*Nannomys*) sp (p).⁵

According to biogeographical data (Rosevear 1969; Petter & Matthey 1975), two species of *Mus* (*Nannomys*) (*M. setulosus* Peters 1876 and *M. musculoides* Temminck 1853) occur in the study

⁴ *Mastomys* in Sierra Leone have commonly been referred to *M. natalensis* (e.g. Demartini, Monath & Monath 1975). According to Petter (1977) and Robbins & Van der Streaten (1989), the correct designation is *M. erythroleucus*.

⁵ The assignment of *Mus setulosus* and *M. musculoides* to the sub-genus *Nannomys*, rather than *Leggada* follows the work of Catzefflis & Denys (1992) and the opinion of Grubb *et al.* (1998).

area (Grubb *et al.* 1998). They proved difficult to distinguish in the hand.⁶ Eighty three *Mus (Nannomys)* sp (p.) were trapped, making it the most commonly trapped taxon (60% of the catch). Forty were adults, of which 23 could be identified with certainty (10 *M. setulosus*, 13 *M. musculoides*). The remainder of the adult specimens exceeded the dimensions given by Rosevear (1969) and by Petter & Matthey (1975) in their diagnostic keys to the genus and did not fit the dimensions given by Hutterer *et al.* (1992). The current study follows Adam (1977) and Cross (1977) in combining data on the two species and referring to them as *Mus (Nannomys)* sp (p).

Specimens of *Mus (Nannomys)* sp (p.) were recorded from all habitat types, but 29 (35%, N = 83) of the records were either from open areas or those with sparse ground cover. Jeffrey (1977) recorded *M. musculoides* from secondary bush, abandoned and unused fields and around buildings, but found it rare in immature cocoa groves and absent from mature ones. Martin & Dickinson (1985) found *M. musculoides* was trapped more often in areas with sparse vegetation. Hutterer *et al.* (1992) found *M. musculoides* to be a grassland creature, while *M. setulosus* inhabited forests. All of the identified adult specimens in the current study showed these habitat preferences. Three adult *M. musculoides* taken in cocoa groves were caught in poorly vegetated areas. A number of very small *Mus (Nannomys)* sp (p.) were caught, 15 (18.07%, N = 83) weighing eight grammes or less. The lightest capture was three grammes. This indicates that, while only a small proportion of trapped *Mus (Nannomys)* sp (p.) were pregnant or lactating (8 = 9.6%, N = 83), reproductive activity may well have been taking place for several weeks prior to trapping. This profile probably reflects the rapid growth of young and the almost continual breeding that is a feature of this species (see Delany 1986).

Praomys tullbergi (Thomas 1894)

This was the second most commonly trapped species, comprising nearly 20% of the catch (see Table 2). It was caught most commonly on the ground in dense vegetation in cocoa groves, although it was caught in all habitats except *Penni-*

setum grassland. *P. tullbergi* is thought to be primarily terrestrial though it "sometimes climbs in small shrubs and creepers within a few meters of the ground" (Happold 1987, p. 140). Happold (1987) and Funmilayo & Akande (1979a) found *P. tullbergi* to be rare in cultivated fields and where grass forms the dominant cover, but common wherever there is tree cover. It is often the most common rodent trapped (*e.g.* see Anadu 1979; Cross 1977; Happold 1974; Jeffrey 1973) and it may be abundant wherever there is sufficient cover (Jeffrey 1977).

Twelve of the 27 trapped *Praomys* were female. Of these, seven were mature and five reproductively active. This, and the agreement of the size of immatures of both sexes with the age-size classes of Happold (1974) and of Cross (1977), indicate that one peak of reproductive activity may have passed, and trapped adult females would have shortly entered a second. This is supported by the observations of Cross (1977), who recorded the breeding season for *P. tullbergi* to be December-April, the main part of the dry season and the beginning of the wet season, and who found lowest percentage of pregnancies and the highest percentage of juveniles in June and July. Cross (1977) defined a juvenile *P. tullbergi* as one weighing less than 25 g. Current results are in accord with this definition, with only one mature individual (a lactating female, 21.5 g) being below it.

Uranomys ruddi (Dollman 1909)

A single specimen, a pregnant female, was trapped in a run among dense stems of a natural near monoculture of *Pennisetum grass*, a typical habitat (Bellier 1968; Grub *et al.* 1998).

Discussion

Trap success

The mean (uncorrected) trap success of this study (3.19%) lies within the lower third of the range of trap successes reported by other studies in the tree-dominated habitats of tropical Africa (see Table 6).⁷ Anadu (1979) found that bait type has considerable influence on trap success and a

⁶ Happold (1987) lists West African specimens of this species as '*M. minutoides*'. We follow Hutterer *et al.* (1992), who pointed out that, while the type locality for *minutoides* is the Cape of Good Hope, South Africa, that for *musculoides* is the Guinea Coast, West Africa.

⁷ the uncorrected value has been used for comparisons because none of the authors of the papers cited in Table 6 mention that they had corrected for sprung traps.

Table 6. Comparative trap success' from previous studies of African small mammals.

Author	Habitat	Country	% Trap success (see note 1)	No. of species
Adam (1977)	Lowland moist forest	Côte-d'Ivoire	3.1	19
Anadu (1979)	Derived grassland	Nigeria	3.1	7
Anadu (1979)	Lowland forest edge	Nigeria	14.6	2
Barnett <i>et al.</i> (1996)	Monsoon forest (dry season)	Guinea	1.9	4
Cross (1977)	Primary moist forest	Sierra Leone	10.4	10
Cross (1977)	Secondary moist forest 1	Sierra Leone	12.1	8
Happold (1975)	Secondary moist forest 2	Nigeria	15.7 ^a	9
Happold (1975)	Derived savannah	Nigeria	4.2 ^b	7
Happold (1975)	Lowland rain forest	Nigeria	11.9	3
Iyawe (1988)	Lowland rain forest, teak plantation	Nigeria	4.9	6
Iyawe (1989)	Various forest habitats	Nigeria	6.5	9
Jeffrey (1977)	Mature cocoa grove	Ghana	4.2	11
Jeffrey (1977)	Immature cocoa grove	Ghana	2.5	6
Jeffrey (1977)	Primary forest	Ghana	5.9	10
Makundi (1995)	Gallery forest	Tanzania	2.2	8
Varty (1990)	Gallery forest	Somalia	4.5	5

^a younger forest, open canopy, thick ground cover

^b older forest, more closed canopy, more sparse ground cover

Note 1: In the absence of precise information to the contrary in the text of these papers it is assumed that each of these reported values represents uncorrected trap success value (see also footnote 7).

higher value might have been possible if a different bait had been used.⁸ Loss of bait to non-target taxa also influences trap success (Barnett & Dutton 1995), and the oiliness of the bait used in the current study may have attracted the attention of ants and other invertebrate bait thieves. Driver ants (*Anomma*) were active across several of the groves during the study and doubtless perturbed the rodent communities in the study area (see also Cole 1975). The small number of daytime catches (five, 3.6% of the total), indicates that the species caught are predominantly nocturnal, in keeping with previous studies (see Grubb *et al.* 1998; Kingdon 1997). Eighty-one of the 127 sexed animals were males (64%), with adults predominating (N = 55, 68%). Such dominance is common and is ascribed to the larger range of adult males (Cross 1977).

Diet

Lophuromys showed a high degree of insecti-

vory, agreeing with previous reports by Cole (1975), and Funmilayo & Akande (1979b). Large volumes of sand were recorded in *Lophuromys* stomachs. This has also been recorded by Iwuala *et al.* (1980) and results from the foraging mode of this rodent. A mixture of insects, earthworms and plant matter has previously been reported for *Hybomys* by Funmilayo & Akande (1979b). A broad-based herbivorous diet for *Praomys* accords with other studies (see Kingdon 1997), although, as in the current study, Funmilayo & Akande (1979b) and Taylor (1984) found it also eating insects. *Hylomyscus* was probably taking advantage of the *Elaeis* crop that was ripe at the time of study. Such opportunism is a feature of the species (Happold 1975, 1987). For *Mus (Nannomys)* sp. (p.), a broad spectrum diet with a bias towards herbivory has also been reported by Funmilayo & Akande (1979b) and by Iwuala *et al.* (1980). *Lemniscomys* is considered predominantly granivorous (see Happold 1987; Grubb *et al.* 1998).

⁸ Oilpalm (*Elaeis guineensis*) fruit bait is very attractive to African rodents (e.g. Coe 1975; Cross 1977; Duplantier 1989; Funmilayo & Akande 1979a; Theo Jones, pers. comm.), while Jeffrey (1977) used banana mashed with palm oil. Even *Lophuromys*, predominantly insectivorous, will opportunistically take oil palm fruits (Funmilayo 1975; Grubb *et al.* 1998).

The effect of grove understory vegetation cover on rodent distributions

Work in Ugandan lowland moist forest (Isabajye-Basuta & Kasenene 1987; Kasenene 1984) has shown a positive correlation between the percentage ground vegetation cover and the density, species richness and species diversity of terrestrial rodents. Similar results have been reported elsewhere in Africa. Jeffrey (1977) achieved 7% trap success in farm scrub, compared with 2% on the sparsely vegetated floor of a mature cocoa grove, and found trap biomass was higher in densely vegetated immature cocoa groves than the sparse understory of mature groves. Similarly, Iyawe (1988) caught seven species of rodent in dense understory of a secondary forest, but only two in the sparse understory of a teak plantation. In northern Nigeria, Happold (1970) obtained lowest trap success where agricultural management had removed the vegetative cover. Jeffrey (1977) found rodent densities were low in primary forest and mature cocoa, "both habitats being similar with high shade and low green matter at ground level" (p. 746). Fleming's 1975 review of tropical small mammal biology indicates this pattern occurs commonly for both trap success and trap biomass.

In the current study also, rodent abundance was positively associated with percentage ground vegetation cover both between - and within-habitats. The lowest catch was achieved in the three year old grove (Site 4), where all ground cover had recently been manually removed (see Table 2). The 40-year-old grove (Site 2) was over-mature with a relatively open canopy and a correspondingly dense ground layer and understory, consistent with the high number of rodents captured there. Site 1 had sparse ground vegetation under the dense canopy typical of a 10-year-old cocoa grove (Urquhart & Wood 1975). Fifty percent of the 22 rodents were taken from 4% of the grove area with high proportion of ground-covering vegetation, illustrating within-habitat importance of vegetation cover on small mammal habitat use. Finally, as found in other studies (e.g. Hanney 1965; Jeffrey 1977), the largest trap biomass was found in grassy, treeless habitats (see Table 3).

The correlation between rodent numbers and the percentage of cover may be explained by an increased number of hiding places and/or increased foraging opportunities (see Dueser & Shugart 1978). In Africa, a number of authors

have recorded a positive relation between undergrowth density and the number of ants (Evans 1974), beetles (Nummelin 1989), and general arthropods (Nummelin & Fursch 1992). Given the high degree of insectivory reported among the species of rodents captured in groves (e.g. *Hybomys*, *Lophuromys*, *Mus*, *Praomys*: Cole 1975; Delany 1975, 1986; Happold 1987; Iwuala *et al.* 1980), increased foraging opportunities may offer a partial explanation for the frequency of these species in dense cover. Similarly, Kasenene (1984) has reported a local increase in the numbers of herbivorous rodents in disturbed forests as herb and tree seedlings germinate from the seed bank.

Community composition

Study of the habitat preferences and biogeographic information in Barnett & Prangley (1997), Grubb *et al.* (1998), Kingdon (1997) and Rosevear (1969) show that the habitats studied contained 43% of the predicted small mammal fauna, including 33% of the forest-dwelling species. Explanations are sought below for this proportionality.

Missing species

No shrews were caught. This was probably due to inappropriate baits and trapping techniques (see Brosset 1988; Rahm 1966a; Verschuren & Meester 1977). A number of rodent species predicted on biogeographical grounds (see Barnett & Prangley 1997; Kingdon 1997) were probably not encountered because of their very specific habitat preferences. For example, *Dephomys defua* (Miller 1900) and *Oenomys* are most commonly found in natural clearings (Kingdon 1997), a habitat not encountered in this study, while *Malacomys* appears to favour minimally disturbed habitats (Barnett *et al.* 1996; Cole 1975). The small amount of arboreal trapping conducted probably accounts for the absence of *Graphiurus*, though Gautun (1977) has shown that this animal is more difficult to trap in the rainy season. *Graphiurus* is highly arboreal (Grubb *et al.* 1998). In areas, like the study site, where natural forest is largely absent, the problems of dispersal across intervening treeless zones may also account for the absence of *Graphiurus* from such forest-like islands as cocoa groves. *Hylomyscus baeri* Heim de Balsac & Aellen, 1965 is a little known, and apparently rare, forest-species. The single record for Sierra Leone

(see Grubb *et al.* 1998) is from Panguma, approximately mid-way between Kenema and Saama (see Fig. 1). With nothing known about the species' ecology, it is difficult to conjecture on the reasons for its absence at Saama. Though it is possible that it is a high-forest specialist and can neither disperse to, nor exist in, cocoa groves.

Local comparisons

The species composition of the catch compares well with that of Cross (1977), who trapped an isolated forest remnant at Bambawo, 25 kilometres north of Kenema (Fig. 1). The lack of *Uranomys* and *Lemniscomys* in his sample is a reflection of the lack of grassland habitats in his trapping area. The presence at Bambawo of *Malacomys*, and the higher numbers of *Hybomys* there, probably reflect the less disturbed nature of Cross' study site.

Rodent communities of cocoa grove

The species richness (eight species in cocoa, three in *Pennisetum* grass, five in rice fields) is broadly in line with the results of other studies (Table 6). Taylor (1961) trapped 6 species of rodent in a Nigerian cocoa plantation, of which *P. tullbergi* comprised some 54.5%. Jeffrey (1977) trapped 10 species in immature cocoa groves (cleared from primary forest, six to eight years previously) and six species in mature cocoa groves (under cocoa for around 20 years). The habitat preference data from Saama agrees well with comparative studies by Rahm (1966b) who found *Lemniscomys*, *Mus* (*Nannomys*) and *Rattus* in villages, fields and cleared areas but never in forests. He found *Hylomyscus* only in forests, while *Lophuromys* and *Praomys* occurred in all habitats. In addition, Jeffrey (1977) found *P. tullbergi* to be the most abundant rodent in cocoa groves, its numbers increasing as the tree cover increased. Conversely, as the proportion of grass cover in a habitat increased, *Lophuromys* became more common (Jeffrey 1973).

Mus musculoides is generally considered an animal of open grassy habitats (Happold 1987; Iyawe 1988, 1989; Martin & Dickinson 1985), but will invade immature cocoa (Jeffrey 1977). The presence of *Mus* in mature cocoa groves at Saama is probably explained by the presence of unclassified *M. setulosus* in the catch, a species said to prefer dense shady cover (Adam 1977). The large number of *Mus* (60% of the total) is surprising as

P. tullbergi is commonly recorded as numerically dominant in arable habitats (Adam 1977; Cross 1977; Happold 1974; Taylor 1961). The presence of *Hybomys* and *Hylomyscus* in cocoa groves was also a surprise, since these species are not generally considered to be tolerant of disturbance (Happold 1975, 1977).

From studies in Nigeria, Happold (1975) identified four groups of species: those with limited tolerance for ecological disturbance and confined to lowland forest (*Hybomys*, *Hylomyscus*, *Malacomys*, *Stochomys*); species with moderate tolerance to disturbance that inhabit either (i) forest types and secondary growth (*Graphiurus*, *Lophuromys*, *Praomys tullbergi*, *Mus. setulosus*) or (ii) farmland and savanna vegetation types (*Mastomys* sp., *Uranomys*, *Taterillus gracilis*); and species with broad tolerances (*Mus musculoides*, *Lemniscomys*, *Myomys*, *Tatera*) occurring in savanna, forest edge and farmland. Jeffrey (1973) believes that, prior to extreme human modification of the African savanna and forests of sub-Saharan Africa (Kingdon 1997; Martin 1991), *Praomys tullbergi* was a forest species, while species such as *Lophuromys* were savannah dwellers with a tolerance for lightly wooded areas. The current study supports this: cocoa groves provide the shaded conditions preferred by *P. tullbergi*, while the sparse understory vegetation in old groves approximates to the brushy habitats preferred by *Lophuromys*. The rodent fauna at Saama reflected the capacity of cocoa groves to harbour a rodent fauna of diverse origins; while fields had a wholly savanna-derived rodent fauna (including *Mus musculoides*, *Lemniscomys*, *Uranomys*), the rodent fauna of cocoa groves comprised a mix of savanna-derived species (*Lophuromys*, *Mastomys*, *Mus musculoides*) and those originally from forest habitats (*Cricetomys*, *Hybomys*, *Hylomyscus*, *Praomys*, *M. setulosus*).

Cocoa groves as forest refugia

The forest-derived species present in Saama's cocoa groves are not those that inhabit primary forest, but edge and tree-fall gap specialists that can tolerate disturbance providing there is tree cover and well-developed understory. The savanna-derived group prefers open habitats, but may enter areas with tree cover if the canopy is open enough and there is little shading (see Cole 1975; Delany 1986; Happold 1974, 1975; Isabajye-Basuta & Kasenene 1987; Jeffrey 1977; Kasenene

1984). This composition reflects the dual nature of the groves, combining the architectural and climatic features of early secondary vegetation with the high frequency of disturbance characteristic of agricultural habitats. These results parallel those of Bellier (1965), Greaves (1964), Everard (1966) in oil palm plantations, and of Everard (1968), Funmilayo & Akande (1979a, 1979b), Taylor (1961) in cocoa plantations. It differs from the classification of Happold (1975) only in that *Hybomys* and *Hylomyscus* appear to be more tolerant of disturbance than suggested by his results from Nigeria.

Similarity of cocoa groves to secondary forests

Booth (1958, 1959), Cole (1975) and Happold (1974, 1975) have shown that deforestation is often followed by ingress of savanna-adapted murids into an area. Pomeroy & Ssekabiira (1990) demonstrated a similar pattern for birds. Both found that many forest-adapted species could persist in secondary forest. Cocoa plantations resemble secondary forest in many aspects of the density and vertical distribution of their vegetation (see Johns 1999; Martin 1991), so one may expect some forest murids to persist in them, while purely savanna-adapted species occupy fields and more open areas. Allport *et al.* (1989) describe a comparable pattern for avifaunas from cocoa plantations of the Gola region, close to the Saama study site. This pattern appears to be widespread; similar results have been obtained by Heinan (1992) for leaf litter herpetofauna in Costa Rican cocoa groves, by Estrada *et al.* (1993) for bat communities in Mexican cocoa groves, by Perez (1994) for Neotropical land snails and by Pacheco *et al.* (1996) for the avifauna of cocoa groves in Brazil.

Decher (1997) has shown that isolated sacred groves of trees are important for the conservation of small forest mammals in West Africa. The current study indicates that cocoa groves can act as refugia for forest-adapted rodents in areas where deforestation has been extensive. Despite the dangers of community disequilibrium resulting from habitat fragmentation (see Laurance & Bierregaard 1997; Lynam 1997; Malcolm 1997), it would seem likely that cocoa groves will also play an important role in ensuring the future survival of some species of West African small mammals. Young groves, with denser understory vegetation, may play an especially important role. Whether they are simply a sink habitat for refugees from

destruction or an important source habitat, capable of provisioning new areas (Laurance & Bierregaard 1997) should be the subject of future research.

However, cocoa groves are, at best, small simplified ecosystems capable of supporting only a tiny subsection of the biodiversity of a primary forest. Moreover, they are subject to regular human disturbance and are not a form of climax vegetation. Under such circumstances the ecosystem dysfunction resulting from the effects of reduced size, system simplification and fragmentation results in a lack of the buffering effects that are present in a complex and larger ecosystem (Laurance & Bierregaard 1997). If cocoa groves are revealed to have an important rôle as refugia, it is likely to be limited to smaller, r-selected, components of the forest fauna. It is unlikely to be so either for habitat specialists, for larger forest mammals or for highly arboreal species (*e.g.* *Graphiurus* species) for whom terrestrial dispersal is problematic.

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Appendix I

Other mammals observed during the study

Putty-nosed guenon *Cercopithecus petaurista* (Schreber, 1774), Campbell's guenon *C. campbellii* Waterhouse, 1838 and sooty mangabey *Cercocebus torquatus atys* (Audebert, 1797) were all commonly seen in troops of 5-20 animals. Villagers said that these primates are attracted to the juicy pulp surrounding the beans in a ripe cocoa pod and that monkey damage can amount to 10-20% of annual losses. As a result, monkeys are hunted as agricultural pests. The squirrels *Heliosciurus rufobrachium leonensis* Thomas, 1923 and *Funisciurus pyrrohopus leonis* Thomas, 1905 were seen in cocoa groves. They are also believed to be pests of the cocoa crop. Specimens of *Thryonomys swinderianus* were seen in grasslands and also being prepared for food.