

## Small Mammal Community: Habitat Preference and Effects after Selective Logging

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**Abstract:** The present study of small mammals in a Malaysian tropical forest attempts to gain some insight into the correlation between their habitat preferences. A 10 ha study plot including primary, old regenerating, and riparian forests were established in the Pasoh Forest Reserve (Pasoh FR) and monthly live trapping employing a mark-and-recapture method was conducted over a period of four years. Thirteen out of the 17 species of the small mammals predominating at the Pasoh FR, including moonrat, treeshrew, squirrels, rats and porcupines, were subjected to statistical analysis to determine their habitat preferences. Based on their abundance in the three habitats, they were divided into four categories: 1) primary forest species, 2) regenerating forest species, 3) riparian species and 4) ubiquitous species, with all the squirrel species categorised as primary forest species. Several environmental factors may explain the observed habitat preferences of small mammals. The present results indicated that the primary forest habitat is rich in food resources and spatial heterogeneity, and should thus provide a higher carrying capacity than the other two habitats. Although 40 years have elapsed since selective logging was carried out in the 1950s, there are still distinct differences between disturbed and undisturbed forests with respect to the small mammal community. Food resources and spatial heterogeneity may account for the differences in mammalian community among the habitats.

**Key words:** community structure, long-term population census, small mammals, species composition.

### 1. INTRODUCTION

Most of the studies on mammalian communities carried out in Malaysian forests have been fairly limited in their scope of community ecological concepts (Duff et al. 1984; Harrison 1957; Kemper 1988; Kemper & Bell 1985; Langham 1983; Lim 1970; Lim et al. 1995; Medway 1966, 1972, 1978; Payne et al. 1985; Stevens 1968; Stuebing & Gasis 1989; Zubaid & M. Khairul 1997; Zubaid & Rizal 1995). Some of these studies were based on qualitative (presence/absence) information of species but not on quantitative aspects in terms of population density, while others dealt with a few dominant species only. There were also studies that focussed on the comparison of mammalian fauna in different habitats, but were carried out in study sites far away from each other. Furthermore, in most cases, environmental conditions within the sites were insufficiently described as to infer the factors regulating animal populations in the habitat.

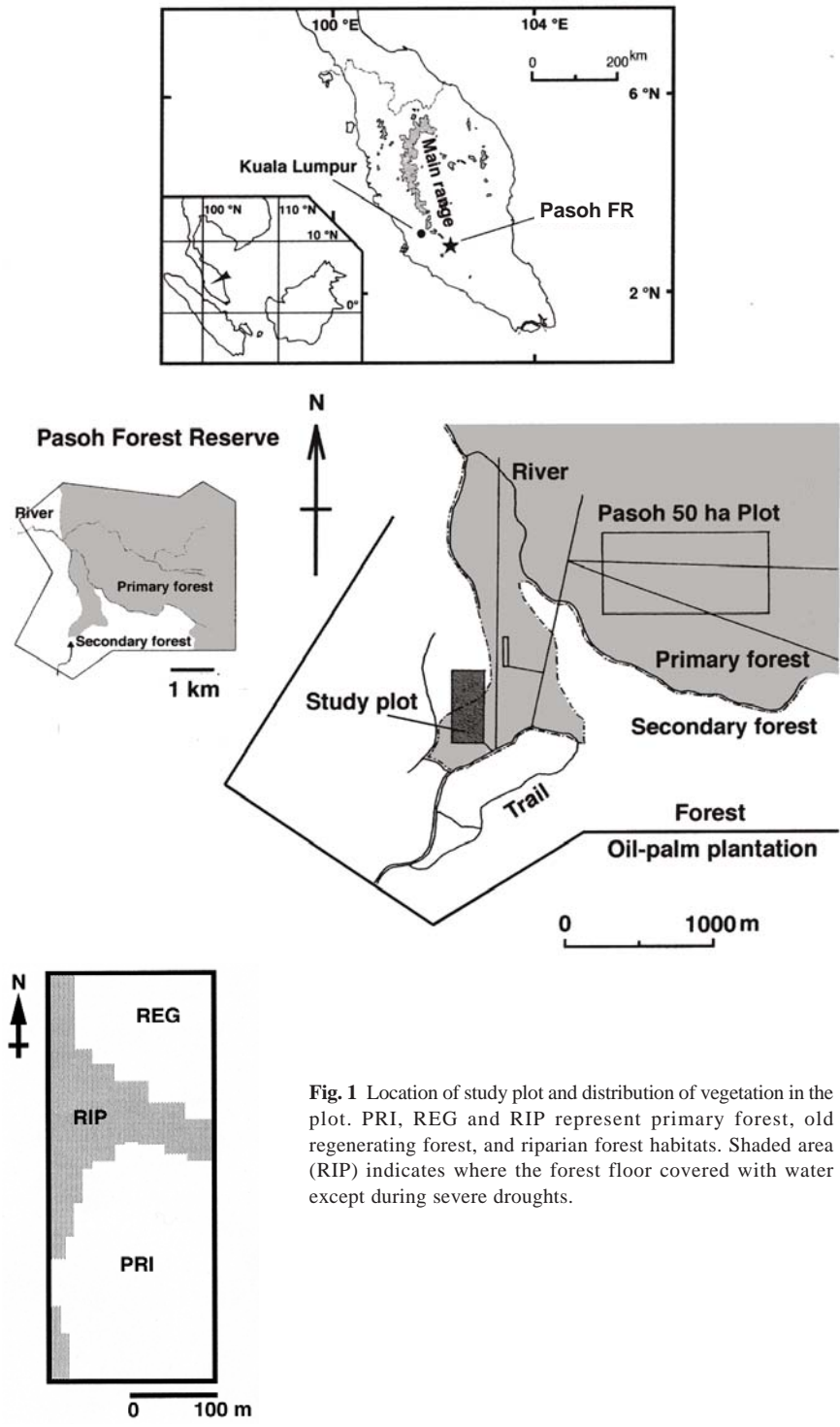
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**Fig. 1** Location of study plot and distribution of vegetation in the plot. PRI, REG and RIP represent primary forest, old regenerating forest, and riparian forest habitats. Shaded area (RIP) indicates where the forest floor covered with water except during severe droughts.

The present study provides more detailed information on species abundance of small mammals in certain habitats in relation to their habitat preference. In this study, surveys of small mammals were carried out in three different forest types, i.e. primary, old regenerating and riparian forests in a Malaysian lowland forest.

## 2. MATERIALS AND METHODS

### 2.1 Study site

A 10 ha (500 m × 200 m) study plot was established in the boundary area between primary and regenerating forests in the Pasoh Forest Reserve (Pasoh FR), Negeri Sembilan, Malaysia (Fig. 1). The study plot consisted of three forest types: primary forest (hereafter PRI), old regenerating forest (REG) and riparian forest (RIP). The PRI habitat is an intact primary forest. The REG habitat is a 40-year regenerating forest that was selectively logged in 1958–1959 under the Malayan Uniform System and has been regenerating naturally (Appanah & Mohd. Rasol 1990; Caldecott 1986; Manokaran & Swaine 1994). The RIP habitat, in this context, is established in an area with small streams running between PRI and REG. It has a water-logged forest floor that occasionally dries out during severe drought. The border areas within 10 m of the water surface were considered RIP habitat, irrespective of forest types. Thus RIP contains the edges of both PRI and REG, though the logging history of RIP is unknown. PRI, REG and RIP in the 10 ha plot accounted for 43.2%, 22.4% and 34.4% of the total area, respectively. The three habitats are adjacent to each other and there were no apparent obstacles blocking the free movement of small mammals within the plot.

### 2.2 Trapping of small mammals

Trapping was carried out monthly from June 1992 to May 1996, during which no mast fruiting event occurred. Two hundred and fifty live-traps were set systematically in a grid design on the forest floor in the 10 ha study plot. The distance between adjacent traps was 20 m. The number of traps in PRI, REG and RIP was 108, 56 and 86, respectively. The size of each trap was 17 cm × 17 cm × 44 cm, for width, height and depth, respectively (made by Environmental Supplies and Services, Selangor, Malaysia). Oil palm fruit (*Elaeis guineensis* Jacq.) was used as bait. One trapping session consisted of four consecutive days. Traps were checked once a day in the morning.

Animals captured were anesthetized with ether and toe-clipped individually for permanent identification. Each animal was identified to species according to Corbet & Hill (1992). At the initial capture of an individual, the following measurements were taken: length of head and body (HB), tail (T), hind foot (HF), ear (E) and body mass (W).

### 2.3 Analyses

A data set was compiled to analyze the habitat use of small mammals. If an individual was captured repeatedly in different habitats in a trapping session, the presence of that individual was allocated among the habitats according to the frequency of captures. For instance, if an individual was captured twice in PRI and once in REG and RIP, the presence probabilities of the individual for that species were allocated as 0.5, 0.25 and 0.25 to the respective habitats. The summation of the presence probabilities for all individuals of the species in a habitat gives the number of individuals captured (hereafter *NI*) of that species in a given habitat in a given

trapping session.

Since disturbance of traps by large animals, e.g. monkeys, was sometimes severe and the intensity was different among habitats, we employed an empirical saturating regression to eliminate the effect of disturbance on the trapping data derived from a ten-day trapping session in the same plot (Yasuda 1998), as

where  $NI_{(i,j)}$  and  $NI_{adj(i,j)}$  are the monthly  $NI$  for the  $i$ th species in the  $j$ th habitat respectively, and  $T_j$  is the total number of effective traps in the  $j$ th habitat in the trapping session. The coefficient of determination ( $r^2$ ) for the regression was 0.992 ( $P < 0.01$ ).

The density of a species in a habitat was determined simply by dividing  $NI_{adj}$  by the area of a given habitat (4.32, 2.24 and 3.44 ha for PRI, REG and RIP, respectively). Biomass in a given habitat was calculated by multiplying the above density by the average body mass of adults of the species.

Based on the four-year average of species density in each habitat (see Table 2), percentage similarity (Whittaker 1952) in terms of the relative abundance of species among the three habitats were calculated between species, and a similarity matrix was obtained. Then the 13 species of small mammals were plotted using the similarity matrix and an ordination method, multidimensional scaling (Kruskal & Wish 1978). SYSTAT for the Macintosh version 5.2.1 (Systat, Inc., Evanston, IL, USA) was used for the analysis.

### 3. RESULTS

#### 3.1 Mammalian fauna

In total, 22 species of mammals belonging to eight families of six orders were recorded in the consecutive four-year censuses. The most dominant order was Rodentia (17 spp.), consisting of 8 spp. of squirrels, 5 spp. of rats, 2 spp. of flying squirrels and 2 spp. of porcupines. Table 1 shows the body dimensions of the most dominant 17 species of small mammals with their locomotion and daily activity cycle. Some arboreal species were frequently captured on the ground. The number of species recorded in PRI, REG and RIP was 17, 15 and 15, respectively. Two species were recorded only in PRI: the Prevost's squirrel, *Callosciurus prevostii* (Desmarest), and the red-cheeked flying squirrel, *Hylopetes spadiceus* (Blyth). Except for some rarely captured species ( $NI_{adj} < 0.5$  individuals month<sup>-1</sup> on average), 13 species of relatively common small mammals were subjected to the analysis below. They were *Echinosorex gymnurus* (Raffles) (Echinaceidae, Insectivora), *Tupaia glis* (Diard) (Tupaiaidae, Scandentia), *Callosciurus notatus* (Boddaert), *Callosciurus nigrovittatus* (Horsfield), *Sundasciurus lowii* (Thomas), *Lariscus insignis* (Cuvier), *Rhinosciurus laticaudatus* (Müller) (Sciuridae, Rodentia), *Rattus tiomanicus* (Miller), *Leopoldamys sabanus* (Thomas), *Maxomys rajah* (Thomas), *Maxomys surifer* (Miller), *Maxomys whiteheadi* (Thomas) (Muridae, Rodentia) and *Trichys fasciculata* (Shaw) (Hystricidae, Rodentia).

#### 3.2 Species composition among habitats

The density and biomass of the 13 species in the three habitats are shown in Tables 2 and 3. There were four remarkable differences in community structure among the habitats. First, total density and biomass decreased in the order PRI > REG > RIP;

$$NI_{adj(i,j)} = \frac{1.37T_j}{T_j + 891} NI_{(i,j)}$$

**Table 1** Body dimensions of small mammals in the Pasoh FR.

Locomotion			Body measurements (mm)										Body mass (g)		N
Activity cycle	Family	Sex	HB	SD	T	SD	HF	SD	E	SD	W	SD			
Species			HB	SD	T	SD	HF	SD	E	SD	W	SD			
Arboreal															
Diurnal															
<i>Callosciurus caniceps</i>	Sciuridae	female	210	na	190	na	46	na	15	na	225	na	1		
		male	198	6	203	8	47	2	15	1	232	13	3		
<i>Callosciurus prevostii</i>	Sciuridae	female	221	na	240	na	54	na	11	na	324	na	1		
		male	255	na	263	na	57	na	18	na	438	na	2		
<i>Callosciurus notatus</i>	Sciuridae	female	199	8	186	18	44	5	15	1	250	18	8		
		male	197	10	189	14	45	4	15	2	250	23	14		
<i>Callosciurus nigrovittatus</i>	Sciuridae	female	192	3	169	15	41	6	14	3	222	30	3		
		male	206	3	192	21	45	4	16	4	235	16	4		
<i>Sundasciurus lowii</i>	Sciuridae	female	136	11	108	18	33	5	12	2	85	14	12		
		male	141	8	110	9	33	6	12	2	88	12	7		
Nocturnal															
<i>Ptilocercus lowii</i>	Tupaiaidae	female	138	6	183	10	26	2	19	3	55	7	3		
		male	na	na	na	na	na	na	na	na	na	na	0		
<i>Hylopetes spadiceus</i>	Sciuridae	female	150	na	145	na	26	na	15	na	95	na	1		
		male	na	na	na	na	na	na	na	na	na	na	0		
Terrestrial															
Diurnal															
<i>Tupaia glis</i>	Tupaiaidae	female	175	22	162	10	42	3	12	2	134	20	36		
		male	181	12	161	16	42	3	14	2	150	20	22		
<i>Lariscus insignis</i>	Sciuridae	female	185	9	97	31	45	4	13	2	210	16	17		
		male	191	10	110	19	46	2	14	3	211	26	33		
<i>Rhinosciurus laticaudatus</i>	Sciuridae	female	209	12	125	24	43	3	16	3	232	9	6		
		male	217	7	114	24	44	2	17	3	248	24	12		
Nocturnal															
<i>Echinosorex gymnurus</i>	Echinaceidae	female	342	40	254	18	60	4	26	2	837	75	3		
		male	362	15	249	15	62	2	26	2	867	101	3		
<i>Rattus tiomanicus</i>	Muridae	female	141	13	143	15	30	2	16	2	74	15	12		
		male	148	18	143	18	30	1	16	1	83	25	10		
<i>Leopoldamys sabanus</i>	Muridae	female	226	10	358	23	45	2	25	2	331	52	21		
		male	239	19	366	32	47	2	24	2	353	67	50		
<i>Maxomys rajah</i>	Muridae	female	178	na	177	na	37	na	20	na	145	na	2		
		male	190	23	184	14	39	3	20	2	158	17	6		
<i>Maxomys surifer</i>	Muridae	female	167	16	169	17	38	2	19	2	141	50	7		
		male	189	19	187	15	41	1	21	3	159	35	13		
<i>Maxomys whiteheadi</i>	Muridae	female	114	14	96	7	25	1	14	2	44	9	7		
		male	119	10	101	10	26	3	14	2	45	11	25		
<i>Trichys fasciculata</i>	Hystricidae	female	380	na	190	na	62	na	27	na	1680	na	2		
		male	na	na	na	na	na	na	na	na	na	na	0		

HB: Head and body, T: Tail, HF: Hind foot, E: Ear, W: Weight, na: not available.

four-year averages of  $7.31 \pm 1.89$  SD,  $5.43 \pm 1.77$  SD and  $4.75 \pm 1.36$  SD individuals  $\text{ha}^{-1}$  and 1,819, 1,525 and 1,369 g  $\text{ha}^{-1}$ , respectively. Second, the total density of diurnal species, including all the squirrels and the common treeshrew (*T. glis*), were lowest in the REG habitat, in the order PRI (3.13 individuals  $\text{ha}^{-1}$ ) > RIP (2.43) > REG (1.18). The proportion of the diurnal community was only 21.7% of the whole community in REG, versus 42.8% and 51.2% in PRI and RIP, respectively. In contrast, the proportion of the nocturnal community was highest in REG, in the order REG (78.3%) > PRI (57.2%) > RIP (48.9%). This tendency resulted from the relatively high density of *Leopoldamys sabanus* (the long-tailed giant rat) in the REG habitat. Finally, the densities of *Echinosorex gymnurus* (the moonrat) and *Trichys fasciculata* (the long-tailed porcupine) were highest in RIP: 0.31 and 0.10 individuals  $\text{ha}^{-1}$ , respectively. They accounted for 6.5% and 2.0% of the whole community of RIP in terms of density and 19.2% and 11.7% in terms of biomass.

As shown in Table 4, ten species of small mammals showed significant differences in population density among habitats (Friedman test,  $P < 0.05$  for all ten species,  $N = 48$ ) and *Callosciurus nigrovittatus* (the black-striped squirrel) and *Trichys fasciculata* showed marginal significance ( $P = 0.052$  and  $0.090$ , respectively). Wilcoxon signed rank test was used as a post hoc test to examine the preference of species between two habitats. The significance level was set 0.05. All six diurnal species and two nocturnal species of rats, *Maxomys rajah* and *Maxomys whiteheadi*, showed preference for primary forest habitat over regenerating forest habitat (PRI > REG). In contrast, two species of rats, *Leopoldamys sabanus* and *Maxomys surifer*, showed preference for both primary forest habitat and regenerating forest habitat, and avoided the riparian forest habitat (REG > PRI > RIP and REG = PRI > RIP, respectively). *Echinosorex gymnurus* and *Trichys*

**Table 2** Densities and biomass of common small mammals in the three habitats. (Species are sorted in the order of population density in the primary forest habitat).

Species	W (g)	Animal density (individuals $\text{ha}^{-1}$ )						Biomass (g $\text{ha}^{-1}$ )		
		PRI		REG		RIP		PRI	REG	RIP
		mean	SD	mean	SD	mean	SD			
Diurnal community										
<i>Tupaia glis</i>	140	1.07	0.62	0.72	0.62	1.11	0.57	149	101	155
<i>Lariscus insignis</i>	211	0.79	0.46	0.20	0.28	0.66	0.42	167	42	140
<i>Callosciurus notatus</i>	250	0.62	0.29	0.16	0.25	0.33	0.26	155	40	82
<i>Rhinosciurus laticaudatus</i>	243	0.36	0.31	0.06	0.18	0.15	0.19	87	14	36
<i>Sundasciurus lowii</i>	86	0.19	0.27	0.04	0.13	0.10	0.17	17	3	9
<i>Callosciurus nigrovittatus</i>	229	0.10	0.14	0.01	0.06	0.08	0.16	22	2	19
Subtotal		3.13	1.21	1.18	0.74	2.43	0.89	597	201	441
Nocturnal community										
<i>Leopoldamys sabanus</i>	347	2.13	0.72	2.62	0.94	1.30	0.62	739	909	450
<i>Maxomys surifer</i>	153	0.83	0.32	0.77	0.65	0.16	0.22	127	118	25
<i>Maxomys rajah</i>	155	0.44	0.32	0.23	0.26	0.05	0.11	69	36	8
<i>Maxomys whiteheadi</i>	44	0.42	0.28	0.26	0.36	0.29	0.27	18	11	13
<i>Echinosorex gymnurus</i>	852	0.21	0.21	0.26	0.35	0.31	0.27	177	219	263
<i>Rattus tiomanicus</i>	78	0.10	0.16	0.10	0.24	0.12	0.21	8	8	9
<i>Trichys fasciculata</i>	1680	0.05	0.10	0.01	0.07	0.10	0.15	83	24	161
Subtotal		4.18	1.04	4.25	1.41	2.32	0.96	1221	1324	928
Total		7.31	1.89	5.43	1.77	4.75	1.36	1819	1525	1369

**Table 3** Species composition of small mammal community in the three habitats.

Species	PRI		REG		RIP	
	density (%)	biomass (%)	density (%)	biomass (%)	density (%)	biomass (%)
Diurnal community						
<i>Tupaia glis</i>	14.6	8.2	13.2	6.6	23.3	11.3
<i>Lariscus insignis</i>	10.8	9.2	3.6	2.7	13.9	10.2
<i>Callosciurus notatus</i>	8.5	8.5	2.9	2.6	6.9	6.0
<i>Rhinosciurus laticaudatus</i>	4.9	4.8	1.0	0.9	3.1	2.6
<i>Sundasciurus lowii</i>	2.6	0.9	0.7	0.2	2.1	0.6
<i>Callosciurus nigrovittatus</i>	1.3	1.2	0.2	0.1	1.8	1.4
Subtotal	42.8	32.8	21.7	13.2	51.1	32.2
Nocturnal community						
<i>Leopoldamys sabanus</i>	29.2	40.7	48.2	59.6	27.3	32.9
<i>Maxomys surifer</i>	11.3	7.0	14.2	7.7	3.4	1.8
<i>Maxomys rajah</i>	6.1	3.8	4.3	2.4	1.1	0.6
<i>Maxomys whiteheadi</i>	5.7	1.0	4.7	0.7	6.1	0.9
<i>Echinosorex gymnurus</i>	2.8	9.7	4.7	14.4	6.5	19.2
<i>Rattus tiomanicus</i>	1.4	0.4	1.9	0.5	2.5	0.7
<i>Trichys fasciculata</i>	0.7	4.6	0.3	1.5	2.0	11.7
Subtotal	57.2	67.2	78.3	86.8	48.9	67.8
Total	100.0	100.0	100.0	100.0	100.0	100.0

**Table 4** Habitat preference of small mammals. Habitat types shown in table represent the more preferred habitat over another.

Species	Family	Habitat preference			P
		PRI vs. REG	PRI vs. RIP	REG vs. RIP	
Diurnal					
<i>Tupaia glis</i>	Tupaiaidae	PRI	n.s.	RIP	< 0.001
<i>Callosciurus nigrovittatus</i>	Sciuridae	PRI	n.s.	RIP	0.052
<i>Callosciurus notatus</i>	Sciuridae	PRI	PRI	RIP	< 0.001
<i>Lariscus insignis</i>	Sciuridae	PRI	n.s.	RIP	< 0.001
<i>Rhinosciurus laticaudatus</i>	Sciuridae	PRI	PRI	RIP	< 0.001
<i>Sundasciurus lowii</i>	Sciuridae	PRI	n.s.	n.s.	0.008
Nocturnal					
<i>Leopoldamys sabanus</i>	Muridae	REG	PRI	REG	< 0.001
<i>Maxomys rajah</i>	Muridae	PRI	PRI	REG	< 0.001
<i>Maxomys surifer</i>	Muridae	n.s.	PRI	REG	< 0.001
<i>Maxomys whiteheadi</i>	Muridae	PRI	n.s.	n.s.	0.016
<i>Rattus tiomanicus</i>	Muridae	-	-	-	0.825
<i>Trichys fasciculata</i>	Hystriidae	n.s.	RIP	RIP	0.090
<i>Echinosorex gymnurus</i>	Echinaceidae	n.s.	RIP	n.s.	0.023

n.s.: not significant ( $P > 0.05$ )

*fasciculata* showed preference for the riparian habitat over the other two habitats (RIP > PRI = REG). One species, *Rattus tiomanicus*, showed no preference for any of the three habitats (PRI = REG = RIP).

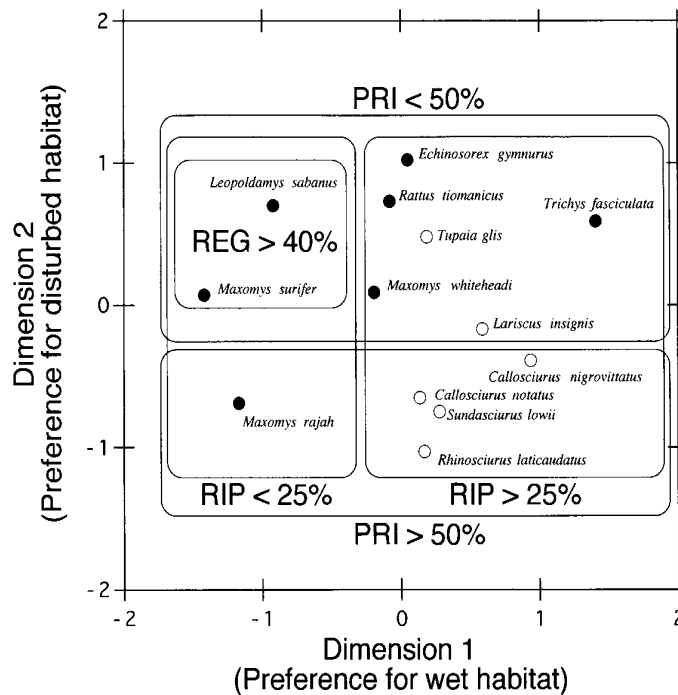
### 3.3 Ordination of species distribution among habitats

The multidimensional scaling performed well (Fig. 2), as the badness-of-fit criterion was 0.020. Relative abundance of species in a certain habitat was shown in the figure. The first dimension related to the relative abundance of species in the RIP habitat, while the second dimension was associated with that in the PRI habitat.

## 4. DISCUSSION

### 4.1 Grouping of small mammals according to habitat preferences

There is no apparent obstacle preventing small mammals from moving freely among the three habitats and no mast fruiting, which may significantly affect small mammal populations, occurred during the study period. Coefficients of variation (CV) on a population density basis were small, being 30.4%, 24.9% and 22.0%, for diurnal,



**Fig. 2** Habitat preference of small mammals. Multidimensional scaling was applied to a percentage similarity index based on relative abundance of species in three habitats. PRI, REG and RIP represent primary forest, old regenerating forest and riparian forest habitats. Percentages shown in figure represent relative abundance of species in the habitat. Open circle: diurnal species, Closed circle: nocturnal species.

Table 5 Summary of the habitat preference of small mammals and some other related factors.

Species group	Family	Locomotion*	Activity cycle*	Density	Habitat preference	Fruit availability	Fallen logs	Canopy gaps	Food habit*
(1) Primary forest species									
<i>Tupaia glis</i>	Tupaidae	Terrestrial	Diurnal	high	PRI = RIP > REG	Positive			insect, fruits
<i>Callosciurus nigrovittatus</i>	Sciuridae	Arboreal	Diurnal	low	PRI = RIP > REG				insect, fruits
<i>Callosciurus notatus</i>	Sciuridae	Arboreal	Diurnal	medium	PRI > RIP > REG				insect, fruits
<i>Lariscus inignis</i>	Sciuridae	Terrestrial	Diurnal	high	PRI = RIP > REG	Positive			insect, fruits
<i>Rhinosciurus laitecaudatus</i>	Sciuridae	Terrestrial	Diurnal	low	PRI > RIP > REG	Positive	Positive		insect
<i>Sundasciurus lowii</i>	Sciuridae	Arboreal	Diurnal	low	PRI > REG	Positive	Positive		insect, fruits
<i>Maxomys rajah</i>	Muridae	Terrestrial	Nocturnal	medium	PRI > REG > RIP				insect, fruits
<i>Maxomys whiteheadi</i>	Muridae	Terrestrial	Nocturnal	medium	PRI > REG	Positive	Positive		insect, fruits
(2) Secondary forest species									
<i>Leopoldamys sabanus</i>	Muridae	Terrestrial	Nocturnal	high	REG > PRI > RIP	Positive			insect, fruits
<i>Maxomys surifer</i>	Muridae	Terrestrial	Nocturnal	high	REG = PRI > RIP			Negative	insect, fruits
(3) Riparian species									
<i>Echinosorex gymmurus</i>	Echinosoridae	Terrestrial	Nocturnal	medium	RIP > PRI = REG				insect, fruits, aquatic animals
<i>Trichys fasciculata</i>	Hystriidae	Terrestrial	Nocturnal	low	RIP > PRI = REG				insect, fruits
(4) Ubiquitous species									
<i>Rattus tiomanicus</i>	Muridae	Terrestrial	Nocturnal	low	PRI = REG = RIP				insect, fruits

\* cited from Medway (1978); and \*\* from Yasuda (1998),  $P < 0.05$ .

nocturnal and whole communities, respectively (Yasuda 1998). This implies that the population density of small mammals in a habitat is rather stable. These data allow us to examine a species' habitat preference based on the differences in population density among habitats.

Eight out of the 13 species (61.5%) showed significant preference for primary forest habitat over regenerating forest habitat, while two species of rats (15.4%) tended to favor the regenerating forest habitat (Table 4). The 13 species of small mammals can be categorized into four species groups; i.e. primary forest species, regenerating forest species, riparian species and ubiquitous species (Table 5). This conclusion was well coincident with that of multidimensional scaling, as two dimensions of habitat preference, one is for wet habitat and another is for disturbed habitat, were important to determine the species composition of small mammals in a certain habitat (Fig. 2). The details of each grouping are as follows:

#### 4.1.1 Primary forest species

This group consists of eight species: *Tupaia glis*, *Callosciurus nigrovittatus*, *C. notatus*, *Lariscus insignis*, *Rhinosciurus laticaudatus*, *Sundasciurus lowii*, *Maxomys rajah* and *M. whiteheadi*. All the diurnal species, including a treeshrew and all squirrels, belong to this group. Their population densities were significantly higher in PRI than in REG (Tables 2, 4), indicating a preference for primary forest habitat.

#### 4.1.2 Regenerating forest species

This group consists of two species of rats, *Leopoldamys sabanus* and *Maxomys surifer*. Their population densities were high in REG as well as in PRI, and low in RIP (Tables 2, 4). Both of these species prefer the primary and regenerating forest habitats to the riparian habitat, which concurs with the findings of Harrison (1957) and Lim (1970).

#### 4.1.3 Riparian species

This group is represented by the moonrat and a porcupine, *Echinosorex gymnurus* and *Trichys fasciculata*, respectively. They showed a higher density in RIP than in the other two habitats, though they were captured in all the habitat types (Table 2). The population density of *E. gymnurus* was significantly higher in RIP than in PRI (Tables 2, 4). This agrees with the findings of Lim (1967) and Medway (1978) in which *E. gymnurus* was usually trapped near streams and preferred swampy forest. The population density of *T. fasciculata* tended to be higher in RIP than in the other two habitats (Table 2), though this pattern was only marginally significant ( $P = 0.09$ , Table 4).

#### 4.1.4 Ubiquitous species

A medium-sized rat, *Rattus tiomanicus*, belongs to this group. The species was captured equally in all the forest habitats in the study plot, with a density of 0.10, 0.10 and 0.12 individuals ha<sup>-1</sup> in PRI, REG and RIP, respectively (Table 2). This species seems to be unaffected by either logging disturbance or the water conditions of the forest floor.

Stevens (1968) compiled the available information of the mammalian fauna in various habitats in Peninsular Malaysia and observed that 29 out of 51 species (56.9%) of small mammals were confined to primary forests. The results of the present study, based on statistical analysis, showed 61.5% (8 out of 13) of small

mammal species are primary forest dwellers confirmed his observation. Previous studies by other researchers also showed that most of the Malaysian small mammals prefer primary forest habitat (Harrison 1969; Lim 1970; Zubaid & M. Khairul 1997; Zubaid & Rizal 1995). Thus, the present study further confirmed the observations of previous researchers.

## 4.2 Potential factors affecting the distribution of small mammals

### 4.2.1 Primary forest species

Yasuda (1998) found that the availability and diversity of fruits was higher in PRI than in REG in the Pasoh FR. Lavelle & Pashanasi (1989) showed that the biomass of ground invertebrates is larger in a primary forest than in an old regenerating forest in Peruvian Amazonia. As most terrestrial mammals are omnivorous (Harrison 1961; Lim 1970; Medway 1978, summarized in Table 5), the primary forest habitat should be rich in food.

Secondly, the density of large fallen logs on the forest floor was higher in PRI than in REG (Yasuda 1998). As most terrestrial small mammals nest in fallen trees or hollows under dead trees (Medway 1978), the abundance of large fallen logs in PRI thus provide more foraging, hiding, resting and nesting sites for them. Furthermore PRI habitat was characterized by well-developed canopy (vertical) structure of the forest (Yasuda 1998). It can be concluded that the primary forest habitat is rich in food resources and spatial heterogeneity, and therefore can provide a higher carrying capacity for small mammals, both arboreal and terrestrial.

### 4.2.2 Regenerating forest species

*Leopoldamys sabanus* and *Maxomys surifer* were common in both disturbed and undisturbed forest habitats (Table 4). Apparently, these species are not so dependent on fallen logs as a resource for nests because they usually nest underground (Lim 1970). This implies that these species can survive in disturbed forest habitats with fewer fallen logs, but may not inhabit areas covered with water. These two species seem to be pre-adapted to disturbed environments.

### 4.2.3 Riparian species

*Echinosorex gymnurus* is known to prefer swampy forests or areas nearby streams as habitat (Lim 1967; Medway 1978). A telemetric study in the Pasoh FR revealed that *E. gymnurus* nests underground in dry places both in PRI and REG, but not in RIP (Yasuda, unpubl. data). They have two or more nests and move among them frequently at intervals of several days. This species is said to depend on aquatic animals for food (Banks 1931; Davis 1962; Gould 1978; Lim 1966, 1967; Medway 1978). Davis (1962) reported that the species feeds mainly on terrestrial invertebrates, such as earthworms, termites, beetles and other arthropods. Wild boars (*Sus scrofa*) intensively dig up the forest floor in wet areas near streams to search for food, probably earthworms (Kemper & Bell 1985; Payne et al. 1985), implying that invertebrate food resources are potentially abundant in the surface soil in this humid habitat. To maintain its large body, *E. gymnurus* may need to search for food over a large area, and the wet area near streams might be an important feeding site for the species.

A telemetric study revealed that *Trichys fasciculata* nests underground in large fallen logs in dry places only (Yasuda, unpubl. data). Using an automatic camera system (Miura et al. 1997), we found that *T. fasciculata* frequently comes to feed on fallen fruits on the ground in RIP as well as in PRI and REG (Yasuda,

unpublished data). Since the species had also been caught in RIP, it is quite probable that *T. fasciculata* utilizes such wet areas as a part of its feeding range.

In addition, the large body size of *E. gymnurus* and *T. fasciculata* (Table 1) may allow them to forage for food in wet areas, perhaps because it insulates them against heat loss when they are wet.

#### 4.2.4 Ubiquitous species

In contrast with the other rats, *Rattus tiomanicus* was captured in both wet areas and in dry forests, and its population density did not differ among habitats (Tables 2, 4). According to previous works, *R. tiomanicus* is a species usually found in cleared land, disturbed or fringing forest (Harrison 1958), but also occasionally in virgin forests (Medway 1972). Harrison (1958) and Sanderson & Sanderson (1964) carried out their studies in grasslands and estimated the size of the home ranges of the species as 73–102 m and 120 m long, respectively. Although Harrison (1958) argued that *R. tiomanicus* has territoriality, our results did not concur. We had 56 catches of 44 individuals of *R. tiomanicus* in total during the four-year census, but 37 individuals (84%) were caught only once. This suggests that, at least in the forest habitat, few individuals of the species stay in their home ranges for more than a few months and that they wander in the forest extensively. Such behavior in forest habitat may account for the ubiquitous distribution of the species found in the present study.

#### 4.3 Effects of selective logging in small mammal community and the forest

As discussed above, there was a large difference in small mammal communities between the primary forest and the old regenerating forest, even though small mammals generally have high reproductive capacity and mobility. With the exception of a few species, the regenerating forest appeared to have a lower carrying capacity for small mammals than the adjacent primary forest. It is obvious that the inferior habitat of the regenerating forest was resulted from the selective logging carried out about 40 years ago. The effects of the logging still remains in the small mammal community there, even though the forest has been untouched since then. It can be concluded that 40 years is still insufficient for small mammal communities of tropical rain forests to recover from the disturbance of selective logging.

Small mammals have the potential to contribute to the seed dispersal of plants through their foraging behavior, i.e. food hoarding (Howe & Westley 1988; Vander Wall 1990). In Malaysian forests, Becker et al. (1985) and MacKinnon (1978) reported that arboreal squirrels hoard fruits at the canopy level, and recently Yasuda et al. (2000) found that some terrestrial rodents in Malaysia also have food hoarding behavior. They are important seed dispersers in tropical rain forests. The present study pointed out that squirrels are among the most vulnerable to logging disturbance in the small mammal community, because they are members of the primary forest species. The loss of dispersal agents as a consequence of logging could reduce the reproductive success of trees in the forest.

#### 4.4 Concluding remarks

It is our firm belief that management plans for tropical rain forests should consider their animal inhabitants as well as trees. Frugivores may contribute little of the ecosystem's energy flow but are essential parts of the ecosystem as seed dispersers.

Logging and forest fragmentation have strong impacts on the frugivore community, even after several decades. In order to restore and maintain the overall vitality of forests, the most necessary and reasonable measure would be to artificially enhance degraded forests to promote better habitats for frugivores. This could be achieved through the construction of corridors to promote animal movement among isolated forest fragments, enrichment of the forest with indigenous fruit-bearing trees, and artificial thinning to improve forest structure.

### ACKNOWLEDGEMENTS

The success of this study owes many things to many people, but in particular to Dato' Dr. Salleh Mohd. Nor, Dato' Dr. Abdul Razak Mohd Ali, Dr. N. Manokaran and Mr. Louis C. Ratnam in Forest Research Institute Malaysia (FRIM). We also thank Drs. Lim Boo Liat, Akio Furukawa, Yoshitaka Tsubaki, Shingo Miura and Kimito Furuta who supported and supervised our work. Special thanks are due to Messrs. Zulhamli Bin Jamaluddin, Ahmad Bin Awang and Adnan Bin Awang for their field assistance in the Pasoh FR.

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