Original article

Effects of selective logging on the microhabitat-use patterns of non-volant small mammals in a Bornean tropical lowland mixed-dipterocarp forest

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Abstract

To assess the effects of habitat disturbance caused by selective logging, the microhabitat-use patterns of six understorey species of small (<1 kg), non-volant mammals in unlogged forests were compared with those in adjacent forests that had been selectively logged 13 and 25 years previously. The study was conducted in a lowland mixed-dipterocarp forest at Tabin Wildlife Reserve, located in eastern Sabah, Malaysian Borneo. Twenty-three microhabitat variables mainly related to vegetation structure, but also including other habitat features, were used to characterise trap-stations set along twenty 200-m long trap-lines equally distributed among four trapping-sites (i.e., five trap-lines per site). The trapping-sites represented two primary and two logged forests. These were arranged as pairs of logged-unlogged forest treatments located at two independent sampling locations. Canonical discriminant function analysis revealed significant separation between trap-stations both occupied and non-occupied by small mammals in the primary and logged forest pair sites at both locations. However, there was no consistent trend observed in the small mammals microhabitat-use patterns in primary compared to logged forests. In general, the small mammals appeared to be able to utilise different sets of microhabitats in different habitat types. Captures in both primary and logged forests were generally positively associated with higher density of fallen logs, twigs and rock piles, number of tree stumps and vegetation cover at the understorey and canopy levels. Wet sites tend to be avoided. These variables seemed to suggest that habitat utilisation by small mammals is closely linked to food or foraging areas and shelter or refuge sites, with probably a strong influence for predator avoidance. Tabin small mammals are able to persist following the first cut in logged forest indicating that although in general, logged forest cannot replace primary forest, selectively logged forests may still constitute an important component for the preservation of small mammal species diversity.

Key words: Small mammals, microhabitat-use patterns, effects of selective logging, North Borneo

Introduction

Owing to the extensive and rapid pace of anthropogenic forest change, particularly as a result of timber extraction for export, many countries in South-east Asia are now running out of sites with primary forest (Danielsen and Heegard, 1995; Whitmore, 1997). A large amount of the remaining tropical forest landscape in this region occurs as a patchwork of small, isolated primary forest remnants in a "sea" of developed land (Corlett and Turner, 1997; Lynam, 1997; Whitmore, 1997; Laidlaw, 2000). Although many studies have generally documented the inferiority of derived habitats as compared to pristine forests for sustaining biological diversity, recent studies have indicated that derived habitats may still have a valuable role. Taking into consideration the level of damage and regeneration time since the last logging, selectively logged forests in the tropics have been found to support quite a significant proportion of original forest faunas, especially when large tracts of undisturbed forests still remain within or close to the logged-over areas (Holloway et al., 1992; Lambert, 1992; Dahaban et al., 1993; Danielsen and Heegard, 1995; Grieser Johns, 1996; Laurance and Bierregaard, 1997; Bernard and Diun, 1999; Robinson and Robinson, 1999; Vasconcelos et al., 2000; Willott et al., 2000; Laidlaw, 2000). In general, although not equal to the original forests in terms of species composition, species richness is usually high in moderately disturbed forest, such as in selectively logged forests, however, specialist species tend to decline (Bernard, *in prep.*).

Since derived habitats increasingly cover much larger areas, and primary forests are correspondingly undergoing reduction and fragmentation, it appears that in the future the survival of many tropical forest faunas must depend more heavily on the management of derived habitats, ideally on a landscape scale that includes some primary habitats. In this respect, it is pivotal to address the issue of whether tropical forest species are able to adapt to significant changes in their natural environment. Knowledge of the habitat requirements of various groups of wildlife is important to their conservation in altered environments, to enable conservation efforts to be concentrated where suitable habitats are present.

Compared to regions like the Neo-tropics and Australian tropics, there are generally few published papers concerning the effects of human-induced habitat disturbance on various groups of tropical forest fauna from Southeast Asia (Cuarón, 2000; Sodhi and Liow, 2000). In this paper I present the results of a study on the effects of tropical rain forest disturbance, in the form of selective logging, on the microhabitat-use patterns of small (< 1 kg) non-volant mammal species. The study was carried out in a tropical lowland mixed-dipterocarp forest of Tabin Wildlife Reserve located in the Malaysian State of Sabah, Northeast Borneo (Figure 1). Specifically, I describe the microhabitat-use patterns of the non-volant, understorey, small mammal community in relatively undisturbed forests and in forests that had been selectively logged 13 and 25 years previously. This was carried out by comparing the microhabitat configurations between trap-stations both occupied and non-occupied by the small mammals at both forest types.

The term "secondary forest" is used in this paper to refer to forest that has grown after the original forest has been selectively logged and may, therefore, to some extent be still dominated by the dipterocarp family. This study formed part of a research project that examined the responses of North-Bornean non-volant terrestrial small mammals to selective logging and the establishment of large agricultural crop plantations (Bernard, *in prep.*).

Materials and methods

Study area

Tabin Wildlife Reserve (5°15'–5°10'N, 118° 30'–118°45'E) is near-rectangular in shape, measures 120,521 ha and is covered mainly with lowland mixed-dipterocarp forest. The north-eastern corner of the Reserve comprises riverine forest, primary brackish water swamp forest and a small amount of mangroves. Topography in most parts of the Reserve is moderately undulating with some steep hills. Elevations range between 100 to 300 m above sea level. The highest peak is 570 m. Mean annual precipitation is 3,100 mm and usually occurs between October–February and May–June. Mean daily minimum and maximum temperatures are 22°C and 32°C, respectively. Many parts of the Reserve were selectively logged during the 1960's to 1980's. When the last logging activities ceased in 1989, only the central part, known as the "Core Area" (8,616 ha) and seven small patches of "Virgin Jungle Reserves" (totalling 2,018 ha) contiguous with Tabin remain undisturbed (Sale, 1994). As a result of this treatment, the landscape at Tabin is composed of a mosaic of different-aged secondary forest habitats (ranging from 11 to 40 years after logging) patched with isolated primary forest remnants. Information of the vegetation structure in Tabin is described elsewhere (Bernard, *in prep.*). The land surrounding the Reserve has been vigorously converted to agricultural crop plantations since the early 1960's. At present Tabin is almost entirely surrounded by large oil palm plantations. The age of the oil palms range from recent plantings to more than twenty years.

Mammal sampling

Sampling was designed to provide quantitative estimates of several aspects of the small mammal community structure in three different forest types: primary lowland mixed-dipterocarp forest, selectively logged lowland mixed-dipterocarp forest and oil palm plantation. Owing to the extremely low number of captures in the oil palm plantation, only data from the

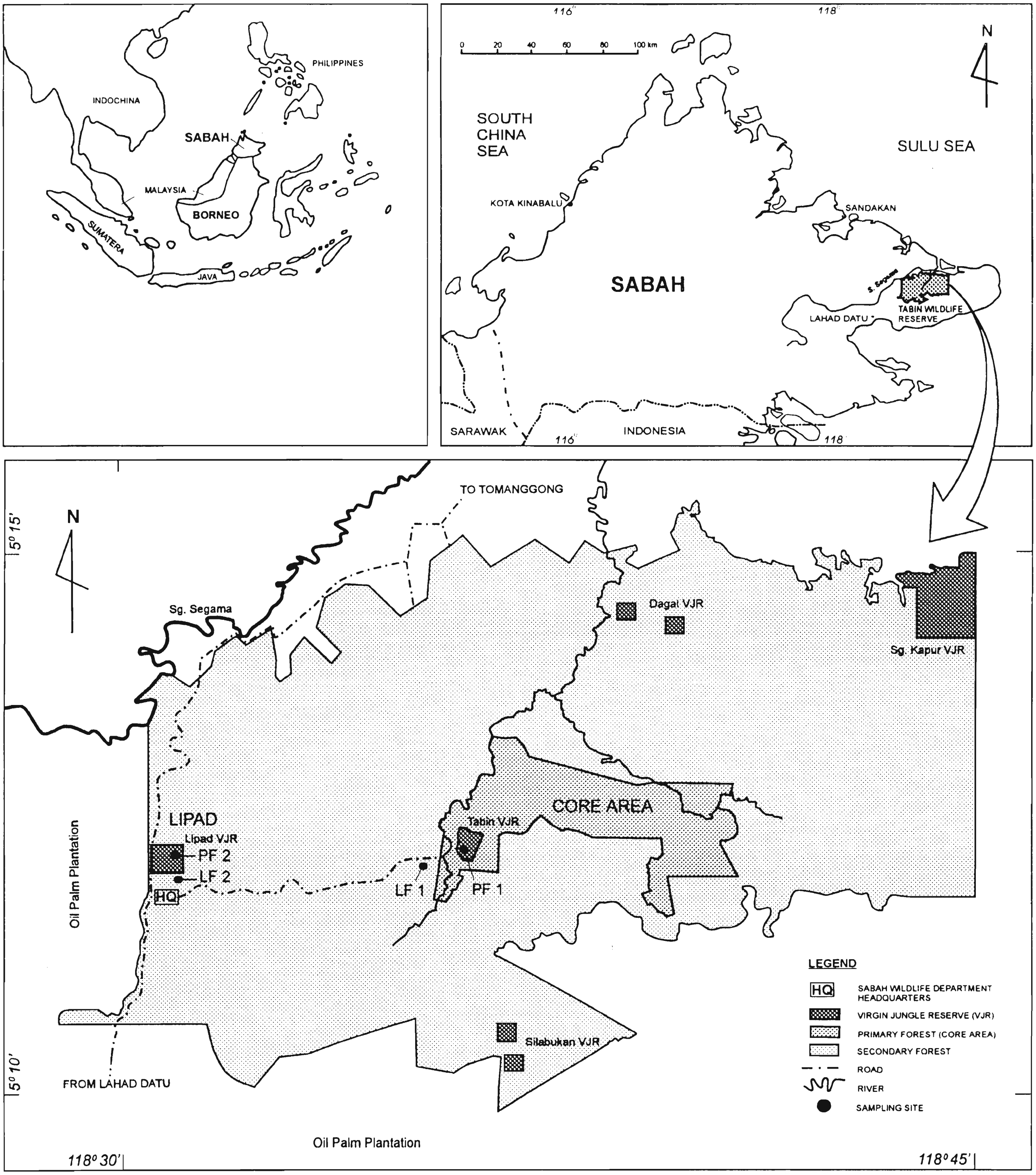

Figure 1. Map of Sabah (Malaysian Borneo) in relation to Southeast Asia, and Tabin Wildlife Reserve in eastern Sabah, indicating locations of trapping-sites at Location 1 (Core Area) and Location 2 (Lipad).

first two forest types and that relates to small mammal species most frequently captured are analysed and presented.

Sampling was confined to two locations, located approximately 20 km apart, within the Tabin area. Location 1 was situated at the Core Area, central part of Tabin, while Location 2 was situated at Lipad on the western side of Tabin near to the border of oil palm plantations (Figure 1). Owing to the wide separation, the two sampling locations were presumed to be independent of each other. Two trapping-sites (≈ 1 km apart), arranged as coupled primary-logged forest treatments, were established at each sampling location. Paired sites were chosen to have generally similar topography and elevation (100–250 m a.s.l). The following abbreviations were used; PF1

Table 1. Twenty-three microhabitat variables recorded at each trap station at Tabin Wildlife Reserve. All variables were assessed in a 2.5 m radius around each trap station.

Stratum		Abbreviation
Over storey		
1.	Canopy cover (%)	CANOPCOV
2.	Canopy height (m)	CANOPHE
Understorey		
3.	Vegetation cover (%) at heights between 1-5m	LOWCOV
4.	Vegetation cover (%) at heights of >5- m	MIDCOV
5.	Woody climber or lianas*	WOODCLB
6.	Palm climber*	PALMCLB
Ground level		
7.	Bare ground (%)	BAREGRD
8.	Vegetation cover (%) at heights between 0-1m (%)	SHRUBCOV
9.	Grass cover (%)	GRASSCOV
10.	Number of vertical stems with gbh => 10 cm	GBH10CM
11.	Number of vertical stems with gbh =>30cm	GBH30CM
12.	Number of vertical stems with gbh =>60cm	GBH60CM
13.	Number vertical stems with gbh =>90 cm	GBH 90CM
14.	Number vertical stems with gbh => 120cm	GBH120CM
Others		
15.	Number of tree stump	STUMPS
16.	Pig damage*	PIGDAM
17.	Logging tracks*	LOGTRACK
18.	Roots*	ROOTS
19.	Areas under water (%)	WATERCOV
20.	Areas covered by rocks (%)	ROCKCOV
21.	Leaf litter cover (%)	LITTERCOV
22.	Fallen logs of => 25cm circumference (%)	FALLENLOG
23.	Small branch and twigs of < 25 cm circumference (%)	TWIGSCOV

* Rank scores: 0—Not evident; 1—Rare; 2—Occasional; 3—Frequent; 4—Abundant.

and LF1 representing trapping sites in primary and logged forests in Location 1; PF2 and LF2 representing trapping sites in primary and logged forests in Location 2. LF1 was selectively logged in 1986 while LF2 was logged in 1974. No detailed information is available on the logging intensity of the logged forest treatments. However, it is quite evident from the remaining stumps that the number of trees extracted at both logged forests are comparable (i.e., ca 8–15 trees per ha) (*per. observ.*). Selective logging in Sabah typically involves felling and extraction of large (usually > 120 cm girth) commercially valuable tree species (Marsh and Greer, 1992). Although only selected trees are felled, more than 45% of the residual stands (smaller trees < 90 cm girth) are also killed or damaged by logging (Aiken and Leigh, 1992)

Small mammals were sampled for five consecutive days and nights per month between October - November 2000 in Location 1 and between February - May 2000 in Location 2. Trapping efforts in Location 1 was smaller due to access difficulty. At each trapping-site the animals were live-trapped using baited wire-mesh live cage traps (17 by 30 by 10 cm) that were set at trap-stations located at 20 m intervals along five 200 m long trap-lines. Baits used were a mixture of cut ripe local variety bananas, pieces of roasted mature coconut kernel and peanut butter suspended on cotton balls (Bernard, 2003). Similar bait mixtures were used at all trapping-sites throughout the study period. Animals caught were individually marked by toe clipping before release.

Microhabitat variables

Twenty-three microhabitat variables relating to vegetation structure, and other habitat features, were used to quantify the heterogeneity of trap-stations (Table 1). Information on all microhabitat variables was collected during the first trapping period of the respective sampling locations. The variables selected were largely those identified in previous studies as good descriptors of microhabitats of understorey small mammal species (e.g. Kemper and Bell, 1985; Patterson, et al., 1990; Lynam, 1997). Changes in these variables are, therefore, expected to influence the patterns of microhabitat usage and local distribution of the small mammals.

Statistical analysis

Prior to analysis all variables were transformed as necessary to correct for non-normal distribution or to improve normality. The following transformation methods were used, logarithmic (base 10) for continuous variables, square root for count variables and arc sine for variables that were recorded as

Table 2. Standardised canonical discriminant function coefficients of 23 microhabitat variables with function 1 (F1) and function 2 (F2)

Habitat variable	F 1	Rank	F 2	Rank
CANOPCOV	**-0.270**	**3**	-0.182	10
CANOPHE	-0.090	15	0.072	17
LOWCOV	**0.224**	**6.5**	**-0.201**	**8**
MIDCOV	-0.013	21	-0.002	23
WOODCLB	0.032	19	**-0.248**	**6**
PALMCLB	**-0.248**	**4.5**	-0.051	19
BAREGRD	**0.684**	**1**	-0.046	20
SHRUBCOV	**0.224**	**6.5**	0.175	11
GRASSCOV	-0.186	8	-0.025	22
GBH10CM	**0.229**	**5**	**0.662**	**1**
GBH30CM	**0.638**	**2**	0.096	16
GBH60CM	-0.068	16	0.198	9
GBH90CM	0.047	17	0.115	15
GBH120CM	0.211	7	**0.215**	**7**
STUMPS	-0.031	20	**-0.277**	**4**
PIGDAM	**-0.248**	**4.5**	-0.051	19
LOGTRACK	0.141	10	**-0.347**	**3**
ROOTS	-0.128	12	0.070	18
WATERCOV	-0.104	13	0.147	12
ROCKCOV	0.130	11	0.118	13
LITTERCOV	0.092	14	**0.275**	**5**
FALLEN LOGS	0.044	18	0.117	14
TWIGSCOV	0.179	9	**-0.392**	**2**

Values in bold (the first eight ranks) highlight variables having the largest contribution to the power of function 1 and function 2.

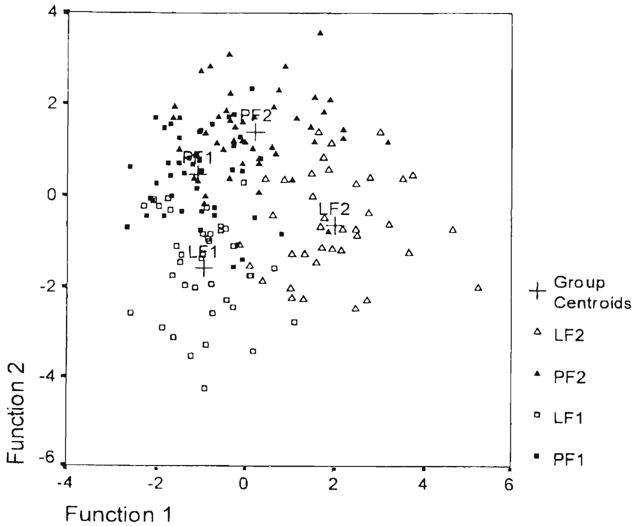

Figure 2. Scatter plot of four trapping-sites based on 23 microhabitat variables analysed using canonical discriminant function analysis [PF1 = trap-stations in primary forest of Location 1; LF1 = trap-stations in logged forest of Location 1; PF2 = trap-stations in primary forest of Location 2; LF2 = trap-stations in logged forest of Location 2].

percentages. Except for variables measured in rank-orders, a value of 1.0 or 0.5 was added to variables with zero scores before making the transformations. It was assumed that the probability of a capture of an individual at a particular trap-station is not influenced by previous and/or following individual captures, i.e., captures at a particular trap-station are independent events. Test of independence of capture locations conducted for data collected during the initial phase of this project showed that captures are independent events (Bernard, 2003).

To describe the microhabitat-use patterns of the small mammals in primary as compared to logged forests, canonical discriminant function (CDF) analysis was performed. Before running the analysis, the discriminating variables were tested for multicollinearity to eliminate highly correlated variables from subsequent analyses. Maximum variable correlations did not exceeded r = 0.80, therefore, all variables were retained.

Separate CDF analyses were carried out for Location 1 and Location 2. Occupied and non-occupied trap stations were treated as the grouping variable, while all 23 microhabitat variables gathered at all trap-stations were treated as the discriminating variables. Prior to running the analysis, the microhabitat configurations of the small mammal species at each location were analysed separately (using CDF analysis). In this initial analysis, small mammal species were treated as the grouping variable, while all 23 microhabitat variables recorded at the respective species capture stations were treated as the discriminating variables.

No significant differences in the microhabitat configurations between small mammal species were found in Location 1 (Wilks' λ = 0.167, χ^2 = 111.095, df = 92, P < 0.085). Likewise, no significant differences in the microhabitat configurations between small mammal species were found in Location 2 (Wilks' λ = 0.463, χ^2 = 57.345, df = 69, P < 0.8411). With these findings, at a particular sampling location and habitat type, the microhabitat variables data at all capture-stations of all species were combined. Thus, in this study the microhabitat-use patterns of the small mammals at a particular sampling location and habitat type refers to the combined microhabitat-use patterns of all of the small mammal species captured.

Owing to the creation of natural tree-fall gaps and the unexpectedly high frequency of wild elephant movements in the forest during the study period, the microhabitat structures at/or within the immediate areas of 34 (or 17% of the total 200) trap-stations, at both Location 1 and Location 2, changed markedly. It was presumed that the small mammals might shift their preferences or ranging patterns in relation to the affected trap-stations. Hence, these stations were

Table 3. Captures and summary statistics for six most frequently trapped small mammal species in primary (PF) and logged (LF) forests at two sampling locations at Tabin Wildlife Reserve

	Location 1 (Core Area)		Location 2 (Lipad)		
Species	PF1	LF1	PF2	LF2	N (ind.)
Maxomys surifer	17 (37)	12 (22)	15 (53)	11 (27)	55
Tupaia glis	2 (2)	6 (11)	7 (12)	6 (12)	21
Niviventer cremoriventer	1 (2)	5 (5)	6 (7)	7 (19)	19
Maxomys whiteheadi	0 (0)	2 (2)	7 (11)	6 (7)	15
Tupaia tana	8 (9)	5 (9)	2 (3)	0 (0)	15
Leopoldamys sabanus	1 (2)	6 (18)	0 (0)	0 (0)	7
No. of individuals (observations)	29 (52)	36 (67)	37 (86)	30 (65)	
No. of trap-nights [a]	500	500	1000	1000	
% trap-succeess [b]	10.4	13.4	8.6	6.5	

(#)—No. of observations or capture events

[a]—No. of traps multiply by no. of nights traps were set

[b]—Percent no. of observations divided by no. of trap-nights

excluded from all analyses mentioned in this paper. All statistical analyses were conducted with SPSS for Windows (Norusis, 1994). A probability of $P \leq 0.05$ was considered significant in all analyses.

Results

Differences in microhabitat structure between trapping-sites

The relative contribution of each of the microhabitat variables (with all other variables present) to the power of the discriminant functions are given in Table 2. On average the four trapping-sites differed by location (Figure 2; along the first canonical discriminant axis, F1) and by forest type (along the second canonical discriminant axis, F2) (Table 2). Both discriminant functions (F1 and F2) explained 46% and 40% of the total variation in the data, respectively, and were significant (Test of functions 1 through 3: Wilks' $\lambda = 0.128$, $\chi^2 = 313.257$, df = 69, $P < 0.0001$; Test of functions 2 through 3: Wilks'$\lambda = 0.316$, $\chi^2 = 175.733$, df = 44, $P < 0.0001$). The number of cases correctly classified was 82% (136 of 166).

Irrespective of forest type, the first discriminant function indicates that Location 1 had greater canopy cover, higher density of palm climber and more obvious signs of pig damage. Location 2 was characterised by very patchy ground cover; with greater coverage of bare ground in some parts, while others had a higher density of shrubs and small sized trees. The forests in Location 2 also had greater vegetation cover at low heights, thus, giving a generally more disturbed impression when compared to the forests in Location 1.

At both locations, the primary forest sites differed from the logged forest sites with the former having the higher density of small (10 cm gbh) and very large trees (120 cm gbh), and more leaf litter, while the latter were characterised by the presence of logging tracks, denser woody climbers, and vegetation cover at low heights. Additionally, the logged forest sites had a greater number of stumps and twigs on the forest floor.

Overall captures

Data for the six most frequently caught small mammals (accounting for > 95% of the overall captures) in the forest habitats of Tabin are presented in Table 3. A total of 119 captures comprising 65 different individuals of all six species were recorded at Location 1. *Maxomys surifer* constituted the largest number of captures (59, 50% of the total) and individuals (29, 46%). Overall trap success for Location 1 was 11.9 (calculated as the number of captures made per 100 trap nights). One hundred and fifty-one captures comprising 67 different individuals of five species were recorded at Location 2. *M. surifer* was again the most abundant (80 captures, 26 individuals), representing 53 % of the total captures and 39 % of total individuals. Overall trap success for Location 2 was 7.6%.

Small mammals microhabitat-use patterns in primary compared to logged forest

A. Location 1 (Core Area)

Table 4. Percentage of variation explained by the first two canonical discriminant functions for Location 1 (Core Area) and Location 2 (Lipad)

Function	Eigenvalue	Percent of variance	Cumulative percent of variation explained	Significance level
		Location 1		
1	1.799	67.5	67.5	F1 –F3 * * *
2	0.623	23.4	90.9	F2 –F3 * * *
		Location 2		
1	1.949	82.4	82.4	F1 –F3 * * *
2	0.676	13.3	95.7	F2 –F3 *

F1 – F3 = Function 1 through Function 3

F2 – F3 = Function 2 through Function 3

* * * P < 0.0001 * P < 0.05

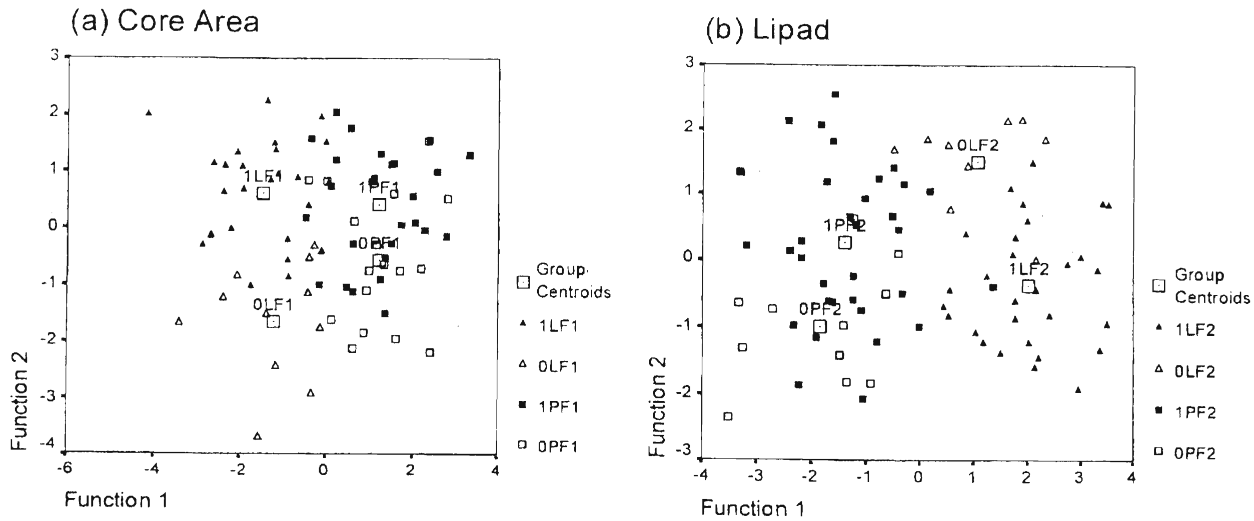

Figure 3. Scatter plots of capture and non-capture stations in primary and logged forest trapping-sites at two different sampling locations i.e., (a) Location 1 (Core Area); and (b) Location 2 (Lipad). The plots were based on 23 microhabitat variables analysed using canonical discriminant function analysis.

0PF1 = NON-CAPTURE STATIONS in primary forest at Location 1;
1PF1 = CAPTURE STATIONS in primary forest at Location 1;
0LF1 = NON-CAPTURE STATIONS in logged forest at Location 1;
1LF1 = CAPTURE STATIONS in logged forest at Location 1;
0PF2 = NON-CAPTURE STATIONS in primary forest at Location 2;
1PF2 = CAPTURE STATIONS in primary forest at Location 2;
0LF2 = NON-CAPTURE STATIONS in logged forest at Location 2;
1LF2 = CAPTURE STATIONS in logged forest at Location 2.

The total number of captures of all species combined did not differ significantly between PF1 and LF1 (Chi-squared goodness of fit test: $\chi^2 = 1.891$, df = 1, P = 0.169). The number of occupied trap-stations was 55 (i.e., PF1 = 28; LF1 = 27), while unoccupied trap stations was 28 (i.e., PF1 = 17, LF1 = 11). The microhabitat configurations between occupied and non-occupied trap-stations at PF1 and LF1 were significantly different (Wilks' $\lambda = 0.177$, $\chi^2 = 118.492$, df = 69, P < 0.0001). The resulting discriminant functions correctly classified 76% (63 of 83) of the trap-stations to group classes. Three discriminant functions were extracted. The percent of total variance explained by the first two functions combined was 90.9% (Table 4). The microhabitat characteristics of the trap-stations used and avoided by the small mammals in PF1 and

Table 5. Standardised canonical discriminant function coefficients of 23 microhabitat variables with function 1 (F1) and function 2 (F2) for Location 1 (Core Area), and Location 2 (Lipad), respectively.

	Location 1				Location 2			
Habitat variable	F 1	Rank	F 2	Rank	F 1	Rank	F 2	Rank
CANOPCOV	**0.359**	**4**	0.264	9	-0.177	15	**-0.422**	**4**
CANOPHE	0.149	18.5	-0.166	11	-0.211	13	-0.076	18
LOWCOV	-0.176	17	**0.390**	**3**	0.162	16	**-0.528**	**3**
MIDCOV	0.227	16	-0.025	22	-0.210	14	**0.332**	**7**
WOODCLB	**-0.387**	**3**	0.092	18	**0.324**	**7**	0.051	21
PALMCLB	**0.328**	**7**	0.071	19	0.086	17	0.172	13
BAREGRD	**0.337**	**6**	-0.256	10	**1.028**	**1**	**0.642**	**2**
SHRUBCOV	-0.255	14	0.129	16	-0.059	19	0.273	10
GRASSCOV	0.115	20	-0.048	21	0.047	21	-0.110	14
GBH10CM	**0.351**	**5**	-0.019	23	**-0.505**	**3**	**0.687**	**1**
GBH30CM	0.149	18.5	**0.325**	**7**	**0.451**	**4**	-0.179	12
GBH60CM	**0.326**	**8**	**-0.359**	**5**	**-0.340**	**6**	0.256	11
GBH90CM	0.144	19	**0.274**	**8**	-0.067	18	0.056	20
GBH120CM	0.312	11	-0.150	12	-0.021	23	-0.086	17
STUMPS	-0.275	13	-0.139	13	0.249	12	**-0.419**	**5**
PIGDAM	-0.323	9	0.135	14	0.029	22	-0.016	23
LOGTRACK	**-0.442**	**1**	-0.050	20	0.260	11	-0.100	15
ROOTS	0.013	22	**-0.356**	**6**	-0.295	9	-0.024	22
WATERCOV	-0.254	15	**-0.619**	**1**	**-0.564**	**2**	-0.063	19
ROCKCOV	0.318	10	**0.376**	**4**	0.273	10	**0.324**	**8**
LITTERCOV	0.310	12	-0.131	15	**0.322**	**8**	0.098	16
FALLEN LOGS	-0.064	21	**0.531**	**2**	-0.056	20	-0.274	9
TWIGSCOV	**-0.419**	**2**	-0.107	17	**0.404**	**5**	**0.369**	**6**

Values in bold (the first eight ranks) highlight variables having the largest contribution to the power of function 1 and function 2

LF1 are best explained by function 2 (see Figure 3(a)). Function 1 appeared to explain the general differences in habitat structure between PF1 (primary forest) and LF1 (logged forest).

Based on function 2, the small mammals in both primary and logged forests at Location 1 appeared to occur at sites with a higher density of fallen logs and vegetation at low level (Figure 3(a) and Table 5). Sites with higher coverage of rock piles were also preferred, but wet sites generally tended to be avoided.

B. Location 2 (Lipad)

Total number of captures of all species combined was not significantly different between PF2 and LF2 (Chi-squared goodness of fit test: $\chi^2 = 3.227$, df = 1, P = 0.072). Number of occupied and non-occupied trap-stations was 63 (PF2 = 34; LF2 = 29) and 20 (PF2 = 11; LF2 = 9), respectively. The differences in microhabitat configurations between occupied and non-occupied trap-stations in PF2 and LF2 were significant (Wilks' λ= 0.149, $\chi^2 = 130.487$, df = 69, P < 0.0001). The resulting three discriminant functions correctly classified 86% (71 of 83) of the trap-stations to group classes. The percent of total variance explained by the first two discriminant functions combined was 95.7% (Table 4). The differences in microhabitat characteristics between trap-stations used and avoided by the small mammals in PF2 and LF2 are best explained by function 2. Function 1 appeared to explain the differences in habitat structure between primary (PF2) and logged (LF2) forests (Figure 3(b)).

At Location 2, based on function 2, preferred sites by the small mammals in the primary forest appeared to differ from that in the logged forest. The small mammals in primary forest seemed to prefer sites with more bare ground, but with many small trees (Table 5). Sites with higher coverage of twigs and rock piles, and with dense vegetation at the middle storey also appeared to be preferred. In the logged forest, preferred sites seemed to have dense vegetation at low and canopy levels. Sites with many tree stumps also seemed to be preferred in this habitat.

Discussion

In this study, *M. surifer* represented the majority of observations and individuals captured. Therefore, the discussion of microhabitat utilisation by small mammals collectively is very much weighted towards the preferences of this species. Nonetheless, it needs to be stressed that all species considered in this study also inhabit the forest understorey. Differences in the microhabitat-use patterns between species were insignificant suggesting a high level of microhabitat overlap. In general, the species share a common diet of insects, other arthropods and fruits (Davis, 1962; Lim, 1970; Langham, 1983; Payne et al., 1985). Accordingly, it can be assumed that the combined microhabitat configurations of the small mammals addressed in this study may represent, very generally, the microhabitat-use patterns of small mammal community of the forest understorey.

The ecological factors that determine the patterns of local habitat usage and distribution of organisms in the tropics are many and particularly complex (August, 1983; Kemper and Bell, 1985). In the Asian tropics, very few investigators have actually demonstrated clear associations with specific microhabitat variables, especially in a multivariate approach. A study in primary and regenerating lowland mixed dipterocarp forest at Pasoh Forest Reserve in Peninsular Malaysia showed that most small mammal captures occurred on drier sites (Kemper and Bell, 1985). In particular, small mammal captures were found to be positively correlated with the density of rotting logs, leaf litter, emergents and seedlings, and negatively correlated with flooding (Kemper and Bell, 1985). Leaf litter and rotting logs have been associated with food abundance especially for ground-dwelling and semi arboreal species (Davis, 1962; Kemper and Bell, 1985), whereas a rocky habitat, fallen logs and tree stumps provide specific requirements for reproduction, such as refuge sites for nesting and rearing of young (Davis, 1962; Tomblin and Alder, 1998).

Several microhabitat variables have been identified by the present study as significant in determining the presence or absence of small mammal species in logged and unlogged forest sites. These include density of fallen logs and twigs, coverage of rock piles and wet areas, number of tree stumps and vegetation density at low heights (1–5 m), middle heights (> 5 m) and at canopy level. In general these variables are comparable to that identified by Kemper and Bell (1985), which are related to foraging and refuge sites, with probably a strong influence for predator avoidance. Many predators, both terrestrial and aerial, locate their prey by sight. By associating with structures like rock piles, fallen logs, tree stumps, dense ground level vegetation and canopy layering, small mammals will be less visible and can, therefore, rapidly escape from predators (Whitten, 1981; Lagos et al., 1995; Dickman, 1995).

Comparisons of the small mammal microhabitat-use patterns in primary and logged forests at the two sampling locations in this study did not reveal any consistent trend. While there is some evidence at the Core Area (Location 1) that the microhabitat-use patterns of the small mammals did not change with selective logging, results from Lipad (Location 2) indicated that the microhabitats of the small mammals in the primary forest were different from that of the logged forest. This shows that small mammals generally are resilient and capable of adapting to changes in their natural environments. This capability may account for the fact that small mammal species that were recorded in the primary forest sites were also present in the logged forest sites, although in different proportions.

To assess the impact of habitat disturbance by comparing results from two different sites, it is possible that observed differences may be due to the heterogeneity of the physical environment such as local topography and soil substrate, or other pre-disturbance differences between sites. To overcome this problem, a "before and after" experiment conducted at the same area has been suggested as a more desirable approach (Wu et al., 1996; Heydon and Bulloh, 1997). Such opportunity is, however, very rare (Dahaban et al., 1993). The primary and logged sampling sites in the present study were paired and each pair was located close to the other. Hence, differences in environmental factors, other than those related to the effects of logging, are believed to be minimal. Although, there was indeed a general difference in the vegetation structure between the two sampling locations in this study, the differences between the primary and logged forest treatments at a particular location appeared to be related only to the differences occurring as a result of habitat change due to selective logging.

Malcolm (1997) remarked that relative to other taxa, small mammals are adapted to overcome early successional series, or other ecosystems with relatively high disturbance regimes and hence more secondary habitats. Although difficult to envisage, this hypothesis implies that compared with other faunal groups, small mammals may have experienced a significantly different suite of habitats during their evolutionary history (Malcolm, 1997). Although Malcolm's remark was specifically for Amazonian small mammals, the same may be true for small mammals in tropical forests of Southeast Asia. Given that, in the case of Tabin, in addition to the primary forest patches, the prospect of sustaining small mammal species diversity in logged forests is undoubtedly high. It should be emphasised, however, that these forests had been logged only once. Furthermore, the relatively long period that has elapsed since the last logging activities took place (i.e., 13 to 25 years) may have allowed the logged forests to recover much of their original vegetation structure. On whether the small mammals may be able to thrive in this habitat after a second or third logging is unknown. Whitmore (1997), however, remarked that repeated logging, especially at short intervals, is likely to be more detrimental than a single episode of logging. While the present study has shown that logged over forest can still play a vital role in biodiversity conservation, many species especially interior primary forest specialist are still reliant on primary forests for their long term survival. Thus, derived habitats should be maintained only in addition to, and not in place of, areas of primary forest.

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