

Movement trajectories and habitat partitioning of small mammals in logged and unlogged rain forests on Borneo

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Summary

1. Non-volant animals in tropical rain forests differ in their ability to exploit the habitat above the forest floor and also in their response to habitat variability. It is predicted that specific movement trajectories are determined both by intrinsic factors such as ecological specialization, morphology and body size and by structural features of the surrounding habitat such as undergrowth and availability of supportive structures.

2. We applied spool-and-line tracking in order to describe movement trajectories and habitat segregation of eight species of small mammals from an assemblage of Muridae, Tupaiidae and Sciuridae in the rain forest of Borneo where we followed a total of 13 525 m path. We also analysed specific changes in the movement patterns of the small mammals in relation to habitat stratification between logged and unlogged forests. Variables related to climbing activity of the tracked species as well as the supportive structures of the vegetation and undergrowth density were measured along their tracks.

3. Movement patterns of the small mammals differed significantly between species. Most similarities were found in congeneric species that converged strongly in body size and morphology. All species were affected in their movement patterns by the altered forest structure in logged forests with most differences found in *Leopoldamys sabanus*. However, the large proportions of short step lengths found in all species for both forest types and similar path tortuosity suggest that the main movement strategies of the small mammals were not influenced by logging but comprised generally a response to the heterogeneous habitat as opposed to random movement strategies predicted for homogeneous environments.

4. Overall shifts in microhabitat use showed no coherent trend among species. Multivariate (principal component) analysis revealed contrasting trends for convergent species, in particular for *Maxomys rajah* and *M. surifer* as well as for *Tupaia longipes* and *T. tana*, suggesting that each species was uniquely affected in its movement trajectories by a multiple set of environmental and intrinsic features.

Key-words: community structure, forest degradation, small mammal stratification, vertical habitat segregation.

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Introduction

The exploitation of a heterogeneous and patchy environment by an animal is likely limited by its adaptations to

a preferred habitat, where habitat structure and resource distribution determine effective detection and movement towards essential resources. The potential of a species to cope with environmental variability is therefore crucial for species distribution on local to regional scales. This aspect is particularly important for animal communities in tropical rain forests. The diversity and distribution of trees that form the basis for high resource availability and structurally rich habitats, which in turn

affect the occurrence of animals using these resources, varies already within single habitats up to regional and ultimately global scales (e.g. Hubbell 1979; Newberry *et al.* 1992; Potts *et al.* 2002). Consequently, the role of environmental variability in structuring populations and communities has gained much interest among ecologists (August 1983; Eisenberg 1990; Emmons 1995). Recently, environmental variability has become even more important because of the rapid fragmentation and conversion of rain forests (Sodhi *et al.* 2004).

Many generalist species, such as small mammals, that exploit the entire three-dimensional space of a forest and that are characterized by various degrees of niche specificity and climbing activity (e.g. Bourliere 1989; Wells *et al.* 2004), often vary in their responses to anthropogenic driven habitat fragmentation and alteration (Laurance & Laurance 1996; Laidlaw 2000; Malcolm & Ray 2000; Lambert, Malcolm & Zimmermann 2005). Small mammals moving through degraded forests encounter differences in structure (e.g. more dense undergrowth in combination with a reduced canopy stratum) and resources availability (e.g. different floral composition). This results in differences in habitat heterogeneity and patch properties (Cannon, Peart & Leighton 1998; DeWalt, Maliakal & Denslow 2003).

To gain a better understanding how species persist and move through such variable environments is therefore of fundamental importance for the assessment of responses by wildlife to habitat changes and the potential of species to cope with altered forest habitats on a long-term basis. Currently, niche utilization of sympatric small mammals in tropical rain forests has been mainly derived from the relationship of their local abundance and associated habitat features, thus attributing partitioning mostly to structural features (Tomblin & Adler 1998; Shanker 2001; Williams, Marsh & Winter 2002) or floral diversity and resource availability (Adler 2000; Kanowski, Irvine & Winter 2003; Beck *et al.* 2004). The differential use of forest strata by small mammals has been repeatedly reported for both neotropical (Charles-Dominique *et al.* 1981; Janson & Emmons 1991; Malcolm 1995; Cunha & Vieira 2002) and palaeotropical (Malcolm & Ray 2000; Saiful *et al.* 2001; Wells *et al.* 2004) forest sites. However, differential substrate use by syntopic species has been suggested to require a finer scale of segregation than a simple arboreal–terrestrial dichotomy (Charles-Dominique *et al.* 1981).

As most studies of non-volant small mammals are limited to trapping data, they frequently comprise only small-scale sampling of a limited number of (micro)habitats along transects and give an incomplete view of habitat patches and vertical layers used by small mammals. It is very unlikely that the patterns derived from those studies are fully representative of the habitat use of small mammals. This misconception has led to the widespread concept of a rather fixed microhabitat segregation derived mostly from data on local scales. However, recent studies stress the importance of data on larger spatial scales to explain why species might use

a certain type of microhabitat in one location and a different microhabitat in another one (Bowers & Dooley 1993; Jorgensen 2004; Kneitel & Chase 2004). Furthermore, habitat types often form a continuous gradient instead of strictly limited ‘patches’. So far, niche segregation in small mammals has been largely regarded as trade-offs within assemblages caused by environmental constraints on the level of individuals, including local habitat characteristics, resource distribution, and presence of predators (Price & Kramer 1984; Kotler & Brown 1988). Recent advances, however, take the analysis of vertebrate movement patterns in heterogeneous and patchy environments into account with a focus on geographical and/or individual variation (e.g. Morales *et al.* 2004; Austin, Bowen & McMillan 2004).

It is reasonable to assume that movement patterns of animals closely follow the structure of the environment, exhibiting, for example, an increased path tortuosity (divergence from a straight line movement) in dense patches with many obstacles and/or discontinuous structural supports. Furthermore, movement patterns with a broad distribution of long movements alternating with a concentration of shorter moves in favoured patches might be most suitable for movement in heterogeneous rain forests (Viswanathan *et al.* 1999; Ramos-Fernández *et al.* 2004). Such patterns may change with the scale of environmental heterogeneity and its perception by the moving animal (e.g. Johnson *et al.* 2002; Nams & Bourgeois 2004). Furthermore, differences in habitat organization and variability suggest that efficient habitat exploitation requires an adjustment of movement strategies along the vertical axis (Solé, Bartumeus & Gamarra 2005). Consequently, logged rain forest might equally require modified movement behaviours compared with unlogged in response to compositional and physical habitat differences.

Structural path properties (e.g. step lengths and path tortuosity) as well as habitat features along the path may improve our understanding of habitat selection and how individuals exploit their environment. Particularly with respect to generalist and wide-ranging small mammal species, an analysis of movement trajectories in both logged and unlogged rain forest should reveal a separation of species by their substrate use and path properties and should further permit investigating the proximate mechanisms leading to such patterns. This might ultimately contribute to a better understanding of interspecific variation in adaptability to a variable forest environment and explain part of the reasons of the decline or persistence of small mammals in altered rain forest habitats.

Moving efficiently through structurally altered forest types will depend on the potential of a species to adapt to variable environmental parameters with regard to the differences in its utilized habitat range. Overall, the responses of small mammals should differ depending upon the magnitude of the physical constraint faced by the species within or between foraging strata. We

therefore hypothesized that the different physical structure in logged forest should lead to different path trajectories. Because species with a similar habitat use are likely to encounter similar features along their path, we expected further that movement trajectories of ecologically and morphologically similar species should be similarly affected by disturbance in relation to habitat partitioning.

Methods

STUDY AREA

The lowland rain forest in Sabah (Malaysia) in northern Borneo has been extensively logged for timber harvesting and for land conversion to implement agricultural plantations, especially oil palms. Currently, only *c.* 5% of the land surface is protected to some extent. About half (*c.* 48%) of the land area is covered with undisturbed or disturbed forest (Sabah Forest Department, pers. comm.). Our study was conducted in three protected and largely undisturbed, unlogged rain forests (Kinabalu National Park 6°2' N, 116°42' E, Tawau Hills National Park 4°23' N, 117°53' E, Danum Valley Conservation Area 4°57' N, 117°48' E) and three logged forests (Kg. Monggis 6°13' N, 116°45' E, Kg. Tumbalang 6°8' N, 116°53' E, Luasong Field Centre 4°36' N, 117°23' E) (Fig. 1). All of the forest stands comprised at least 1000 hectares; they were 17–236 km apart and situated at altitudes of 200–900 m. The sites in unlogged rain forest are characterized by large numbers of dipterocarp trees rising up to 60 m. Whereas the emergents usually grow with their tree crowns separated from each other, trees

at medium heights (10 and 40 m) form an interconnected and thus light-shielding canopy. The forest floor is mainly covered by saplings. Dense ground vegetation is limited to patchily distributed treefall gaps and other perturbations. In contrast, the sites in logged forest are characterized by smaller trees with heights of less than 25 m as a result of uncontrolled selective logging about 20–30 years prior to our study. Because of the relatively open canopy, the understorey is typically covered by dense vegetation of abundant plant species, such as ginger (Zingiberaceae), climbing bamboo *Dinochloa* spp. and other vines, sago palms *Metroxylon* spp. and rattan *Calamus* spp. This leads to a structurally highly complex habitat within the first few metres above-ground.

ANIMAL HANDLING AND SPOOL APPLICATION

Our study focused on eight small mammal species from the families Muridae, Tupaiidae and Sciuridae (Table 1). All are common and occur in unlogged as well as in logged forests.

We classified all species as terrestrial or scansorial (semiterrestrial, active in the first few metres above-ground) except *Niviventer cremoriventer*, which is active both on the ground and in the canopy, and *Leopoldamys sabanus*, which has been occasionally recorded in the canopy (see Lim 1970; Wells *et al.* 2004).

Animals were captured between September 2002 and November 2004 as part of a mark–recapture study on effects of habitat degradation on small mammals at the six study sites. We conducted 18 trapping sessions of 16 days each, alternating between the different forest sites. Locally made wire-mesh live traps (280 mm × 140 mm × 140 mm) baited with banana were placed on the ground in one transect area of 40 trap stations and in two additional areas well separated from each other (usually 0.5–1.1 km, and somewhat less in Kinabalu Park because of topographic conditions). Captured animals were anaesthetized, measured (HF = hind feet, T = tail, and HB = head–body length) (Table 1) and marked with subcutaneous transponders (AEG Trovan, Identification systems, Germany).

For movement analysis, a spool-and-line device consisting of quilting cocoons of approximately 120 m nylon thread (Danfield Ltd, UK) encased by a heat-shrinking tube (total weight *c.* 1.7 g) was glued with cyanoacrylate (Pattex, Henkel, Germany) on to the fur on the back of selected individuals. Fur loss and minor skin irritations caused by the spool had disappeared in all animals that were recaptured about 2 weeks later. Cocoons with threads of different colours were used to facilitate distinction of individual tracks. The free end of the thread was tied to nearby vegetation and labelled. The threads were usually tracked on the day following the animal's release. As initial movements upon release were sometimes influenced by handling, the first 5–10 m of track were discarded and recordings started after the first subsequent change in direction.

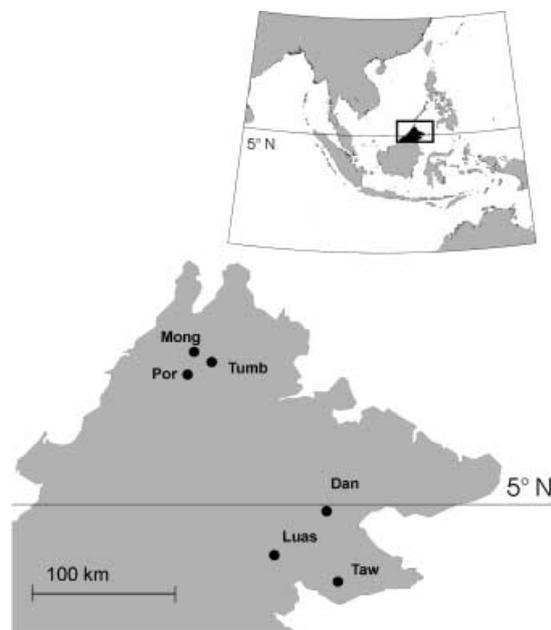


Fig. 1. Map of Borneo with the six study sites. Unlogged forest: Kinabalu NP 'Por'; Tawau Hills NP 'Taw'; Danum Valley Conservation Area 'Dan'; logged forest: Kg. Monggis 'Mong'; Kg. Tumbalang 'Tumb'; Luasong Field Centre 'Luas'.

Table 1. Studied species, their biometric measurements, and the numbers/lengths of spools recovered in unlogged (UF) and logged (LF) forest. Biometric measurements are given as the mean proportions of hind feet (HF) and tail (T) to head–body length (HB) with one SD

Species	Biometric measurements of adults			Spools recovered	
	Weight (g)	HF/HB (mm)	T/HB (mm)	No. in UF/LF	Total length (m)
Long-tailed giant rat <i>Leopoldamys sabanus</i>	368 ± 64 (n = 101)	0.22 ± 0.01 (n = 84)	1.64 ± 0.11 (n = 74)	25/24	2 704
Brown spiny rat <i>Maxomys rajah</i>	160 ± 35 (n = 28)	0.22 ± 0.02 (n = 25)	1.12 ± 0.09 (n = 13)	10/13	1 341
Red spiny rat <i>Maxomys surifer</i>	157 ± 47 (n = 38)	0.24 ± 0.02 (n = 35)	1.16 ± 0.13 (n = 23)	12/4	1 018
Long-tailed tree rat <i>Niviventer cremoriventer</i>	69 ± 13 (n = 142)	0.21 ± 0.01 (n = 144)	1.49 ± 0.09 (n = 108)	9/6	720
Low's squirrel <i>Sundasciurus lowii</i>	96 ± 22 (n = 24)	0.27 ± 0.02 (n = 22)	0.74 ± 0.09 (n = 22)	4/4	448
Large treeshrew <i>Tupaia tana</i>	218 ± 27 (n = 126)	0.25 ± 0.01 (n = 110)	0.93 ± 0.06 (n = 106)	28/31	3 990
Common treeshrew <i>Tupaia longipes</i>	196 ± 25 (n = 59)	0.27 ± 0.03 (n = 51)	1.03 ± 0.07 (n = 50)	26/12	3 069
Slender treeshrew <i>Tupaia gracilis</i>	81 ± 19 (n = 14)	0.30 ± 0.01 (n = 13)	1.31 ± 0.08 (n = 13)	1/3	235
Total				212	13 525

Tracks of animals were marked with plastic poles to determine steps lengths (STEPL) of straight-line sections with similar habitat characteristics and no change in direction. The lengths of these sections were measured with a measuring tape to the nearest 10 cm. Changes in direction between steps were assessed with a sighting-compass (Recta DP 65) to the nearest 2°. Threads were followed until they either ran out, had snapped or had been shed off with the spool. Occasionally, the habitat was too difficult for further tracking including movements in nonclimbable trees and in a few cases movement through very dense undergrowth below treefalls.

During tracking, we classified undergrowth density from 0 to 1 m height for an area of approximately 1 m to the left and the right of the track into four groups: (1) light (ground barely covered; plant cover < 20%); (2) intermediate (ground covered mainly by saplings/small trees with litter still visible; plant cover > 20–70%); (3) dense (litter hardly visible because of high density of saplings and gap vegetation; plant cover > 70–90%); and (4) very dense (surroundings completely covered by dense vegetation, litter not visible, mainly forest gaps;

plant cover > 90%). For movements of the animals above-ground, we additionally recorded type, diameter and maximal height of supportive structures above-ground.

DATA ANALYSIS

Vertical habitat utilization was categorized into five classes (GR: ground; C1: 1–50 cm above-ground; C2: 50–100 cm above-ground; C3: 1–5 m above-ground; C4: > 5 m above-ground). Nine habitat variables were used to characterize the movement of species within the habitats (see Table 2). We analysed habitat variables for species comparison by pooling data from unlogged forest only. Differences in habitat use were further analysed between sites in logged and unlogged forest for all species.

As the scale of our measurements allowed us only to assess proportions rather than absolute values, we used nonparametric Kruskal–Wallis ANOVA and Mann–Whitney *U* statistics for all variables, using Bonferroni correction for *post-hoc* pair-wise comparisons of variables. To evaluate the overall differences of specific

Table 2. Explanations for variables used to distinguish habitat utilization along movement tracks. Analysis of variables was either individual-based (I) or pooled (P). Some variables were analysed with respect to different above-ground classes C1–C4

Variable	Description	Analysis
NCLIMB	Number of climbing up movements/thread recovered (m)	I, C1–C4
ABVGR	Total length of movements above-ground (m)/thread recovered (m)	I, C1–C4
HTMOV	∑ (Step length (m) * height above-ground (m))/thread recovered (m)	I
MAXHT	Maximum height (m) reached	I
LOGMOV	Movement on logs (m)/thread recovered (m)	I
DIAM	Diameter of supportive structures used (mm)	P, C1–C4
UNDENS	Proportion of movement in the various undergrowth classes ((1)–(4))	I
STEPL	Step length (m) (straight-line sections with no directional or habitat-related change)	I
TANGL	Turning angle between consecutive steps	I

Table 3. Mean of variables given as values relative to 100 m of track length averaged for all individuals except for the variables DIAM, STEPL and TANGL, which were calculated as medians for the pooled data

Habitat variable	<i>Leopoldamys sabanus</i>	<i>Maxomys rajah</i>	<i>Maxomys surifer</i>	<i>Niviventer cremoriventer</i>	<i>Sundasciurus lowii</i>	<i>Tupaia longipes</i>	<i>Tupaia tana</i>	<i>Tupaia gracilis</i>
NCLIMB C1–C4 (m/100)	4.4	3.3	3.5	8.4	9.6	5.2	4.9	7.2
NCLIMB C2–C4 (m/100)	2.4	0.4	0.9	6.1	4.2	1.6	1.9	3.1
NCLIMB C3–C4 (m/100)	1.4	0.0	0.4	3.6	2.3	0.6	0.6	0.9
ABVGR C1 (m/100)	9.1	6.3	5.1	8.7	16.7	12.5	9.8	13.2
ABVGR C2 (m/100)	3.8	0.6	1.1	6.8	8.8	3.7	5.9	11.4
ABVGR C3 (m/100)	8.0	0.0	2.3	27.8	11.4	2.7	3.0	6.3
HTMOV (m/100)	31.4	1.8	7.2	96.7	29.7	10.9	12.3	26.9
MAXHT (m)	1.7	0.3	0.6	4.1	1.7	1.0	1.1	1.6
LOGMOV (m/100)	6.5	4.4	2.3	4.6	15.4	9.0	9.0	3.8
DIAM (mm)	10.2	11.6	12.2	5.6	14.8	13.2	13.0	11.1
UNDENS (1) (m/100)	14.5	17.2	15.6	13.9	2.0	11.3	4.4	4.2
UNDENS (2) (m/100)	75.9	69.8	67.5	70.7	79.7	61.6	73.9	52.0
UNDENS (3) (m/100)	9.1	12.5	15.9	14.8	17.9	24.5	20.9	42.7
UNDENS (4) (m/100)	0.5	0.4	1.0	0.6	0.4	2.6	0.9	1.1
STEPL (m)	1.9	1.7	1.8	1.6	1.7	2.1	1.9	1.7
TANGL (°)	47	45	47	60	37	45	47	54

paths used by the species, we applied principal components analysis (PCA) to ordinate means of habitat variables for all tracked species in unlogged forest and separately for the five most intensively tracked species in logged and unlogged forest. These ordinations allowed estimation of differences between species or populations by reducing the entire set of parameters to two descriptors encompassing as much variability as possible. Hence, we were able to evaluate movement trajectories of species and populations in different forest types in relation to each other.

The frequency distributions of step lengths were tested in relation to different movement models by using a log-log regression (see Turchin 1998). For this, we pooled data among forest types and applied a Student's *t*-test assessing differences in regression slopes among species in unlogged forests and among populations in logged vs. unlogged forests. As most individuals moved with persistence in one particular direction and as tracks were assumed to comprise orientated paths, we estimated path tortuosity (*D/L*) as the ratio between the distance from the starting to the final point and the path travelled to reach this distance (see Benhamou 2004).

Results

We obtained a total of 212 movement tracks comprising a total length of 13 525 m from at least 188 individuals (some tracked several times) of the eight focal species. The lengths of individual records varied from 30.1 to 119.1 m (mean 63.8 ± 26.7 m). Additional spooling threads were recovered for a ninth species, the lesser treeshrew *Tupaia minor*. However, this species was not included in our analysis as it spent a large proportion of its activity high in the canopy (> 10 m). Most individuals climbed up vertical trunks or on vines and other supportive structures straight into the canopy after moving a few metres on the ground. This did not permit

proper tracking. Similarly, *N. cremoriventer* also frequently approached the upper canopy. Half of all trial threads (50%) could not be fully recovered.

INTERSPECIFIC VARIATIONS IN MOVEMENT TRAJECTORIES

Movement patterns differed significantly between species with regard to most variables (all Kruskal–Wallis ANOVA $H > 15.8$, $P < 0.05$) (Table 3, Fig. 2), except for the proportion of movement in medium and very dense undergrowth (UNDENS (2), (4)), the movement on logs (LOGMOV) and the number of climbing up movements (NCLIMB C1–C4) (all Kruskal–Wallis ANOVA $H < 13.5$, $P > 0.05$). *Post-hoc* pair-wise species comparisons for all dependent variables revealed 135 variables of 518 (26%) that were significantly describing the movement tracks of the eight species. *Niviventer cremoriventer* ($n = 51$), *Maxomys rajah* ($n = 45$) and *T. longipes* ($n = 36$) accounted for most of these differences. For the closely related species *T. longipes* and *T. tana*, we found only a difference in the diameter of supports used 1–5 m above ground (DIAM C3, Mann–Whitney *U*-tests $U = 432$, $P < 0.018$). We found no differences for *M. rajah* and *M. surifer*.

Similar patterns of species segregation were also obtained from PCA (eigenvalues: $\lambda_1 = 10.83$, $\lambda_2 = 4.38$). The first PCA axis represented a gradient of above-ground activity and explained 54% of variability in the movement patterns, whereas the second axis explained 22% of variability mostly attributable to movements on logs, diameter of supports, and undergrowth density (Fig. 3).

The diameter of supportive structures used by small mammals generally declined with movement heights (DIAM, Kruskal–Wallis ANOVA $H_{n=974} = 100.12$, $P < 0.01$). Vice versa, species that climbed more often than others moved significantly less in light undergrowth

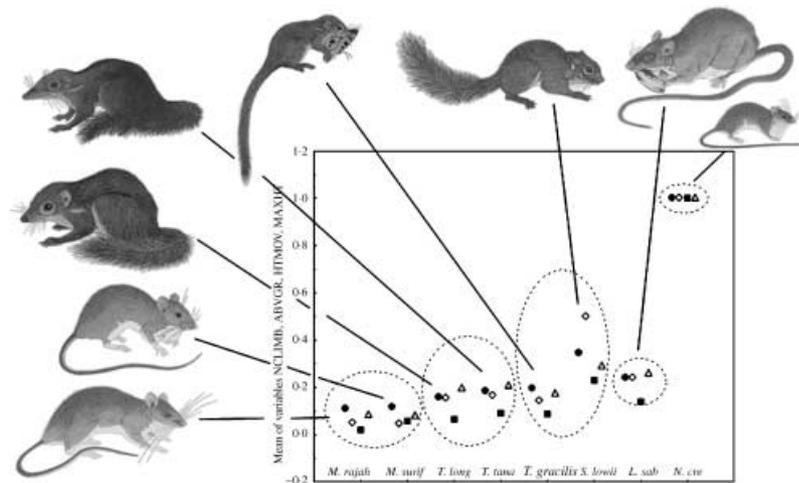


Fig. 2. Mean of variables describing vertical habitat use in eight small mammal species. The three categories (C1–C4) for the variables NCLIMB and ABVGR were pooled so that the mean of all classes were multiplied by class number and an overall mean was calculated. The variables NCLIMB (●), ABVGR (◇), HTMOV (■), and MAXHT (△) are given for all study species. Species with similar habitat use are encircled. The illustrations of the small mammals are reproduced from Payne, Francis & Phillipps (1998) with kind permission from the Sabah Society (Kota Kinabalu, Malaysia).

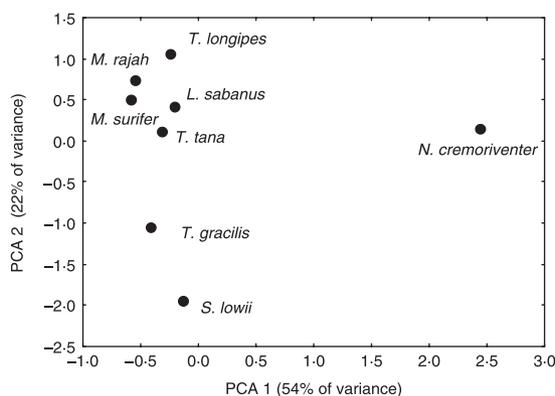


Fig. 3. Principal components analysis (PCA) plot of movement patterns of eight small mammal species based on the means of habitat variables. The first PCA axis represents a gradient in above-ground activity (MAXHT, HTMOV, NCLIMB C2, ABVGR C4), whereas the second axis is mostly explained by LOGMOV, DIAM C2, C3 and UNDENS C2, C1. Eigenvalues: $\lambda_1 = 10.83$, $\lambda_2 = 4.38$.

(NCLIMB C1, Spearman's $R_{n=8} = -0.83$, $P < 0.05$) than in denser undergrowth.

The average body mass of species was positively correlated to step length (STEPL, Spearman's $R_{n=8} = 0.76$, $P < 0.05$). However, we did not find a correlation between body mass and diameter of supports (DIAM, Spearman's $R_{n=8} = 0.17$, $P = 0.69$) or any other variable. The biometric proportion of hind feet to head–body length (HF/HB, see Table 1) was positively correlated with the movements of the species above-ground and the proportion of movement in dense undergrowth (ABVGR C1, UNDENS 4, both Spearman's $R_{n=8} > 0.77$, $P < 0.05$) and negatively to the movement in light undergrowth [UNDENS 1, Spearman's $R(n=8) = -0.73$, $P < 0.05$]. The biometric proportion of tail length to head–body length (T/HF) was negatively related to

the diameter of supports (DIAM, Spearman's $R_{n=8} = -0.93$, $P < 0.01$).

For the five most intensely tracked species, step-length distributions in unlogged forest did not correspond to a probability distribution that could be normalized (regression slopes $-1.15 < \mu < -0.74$ (all $r^2 > 0.37$) (Fig. 4a,b), indicating that random walk models were not applicable to these movements. The frequency distributions of steps lengths (all Student's t -test $t_{v \geq 82} < 1.24$, $P > 0.20$) and path tortuosity (D/L, Kruskal–Wallis ANOVA $H_{n=101} = 11.82$, $P = 0.11$) did not differ among these species, indicating that principal structural path organization was similar among species.

MOVEMENT PATTERNS IN LOGGED VS. UNLOGGED FOREST

All species differed in their movement patterns between logged and unlogged forest, with most changes recorded for *L. sabanus* (Table 4). *Maxomys rajah* and *L. sabanus* travelled significantly longer distances at heights of 1–50 cm in unlogged than in logged forest (ABVGR C1, both Mann–Whitney U test $U > 30$, $P < 0.05$). However, whereas these differences in the above-ground movements at this height indicated more above-ground activity for *M. rajah* in unlogged forest, the opposite was true for *L. sabanus*, which moved on average longer distances (although not significantly) at heights between 1 and 5 m in logged forest and was recorded three times to climb up in the canopy > 5 m in logged forest, but never in unlogged forest. *Niviventer cremoriventer* climbed more often above heights of 50 cm in unlogged forest (NCLIMB C2–C4, Mann–Whitney U test, $U = 8$, $P < 0.05$) and travelled longer distances at heights between 1 and 50 cm in unlogged than in logged forest (ABVGR C1, Mann–Whitney U test, $U = 10$, $P < 0.05$). Whereas *M. rajah* used the above-ground habitat more intensely

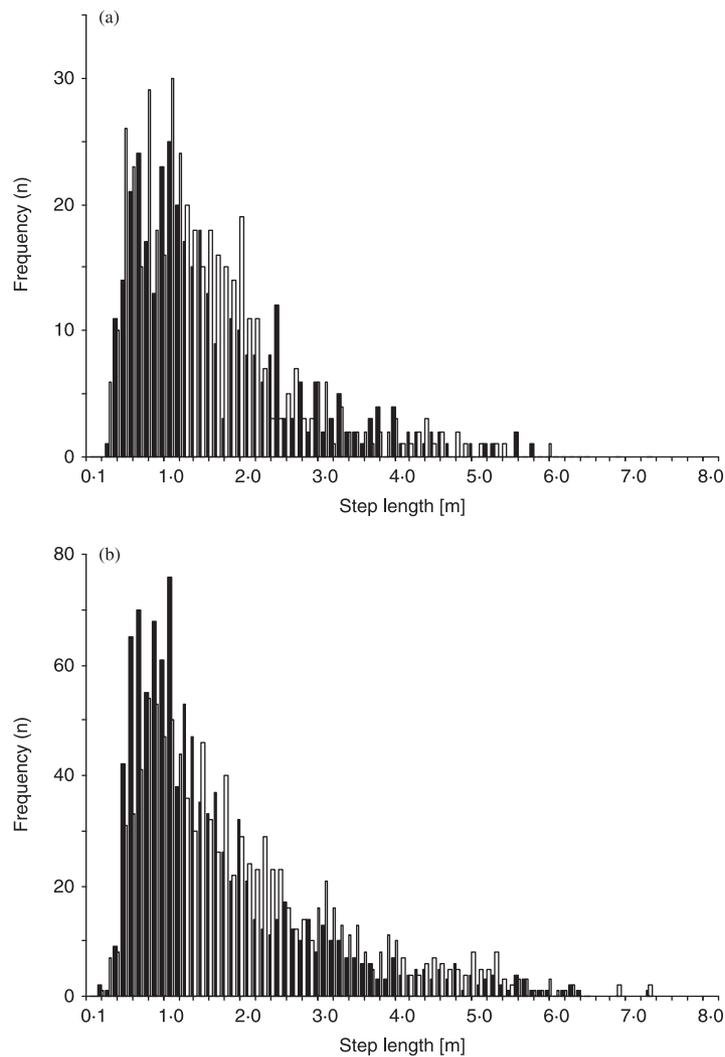


Fig. 4. Frequency distribution of step lengths (STEPL) for *Maxomys rajah* (a), and *Tupaia tana* (b). Distributions are given for movements in unlogged (black bars) and logged (white) forest. Data comprise a total of 804 steps for *M. rajah* and 1090 steps for *T. tana*.

in unlogged forest (HTMOV, Mann–Whitney *U* test, $U = 33.0$, $P < 0.05$) and climbed on average higher up in unlogged than in logged forest (MAXHT, Mann–Whitney *U* test, $U = 27.5$, $P < 0.05$), *T. longipes* used the above-ground habitat more intensely in logged forest

(HTMOV, Mann–Whitney *U* test, $U = 82.5$, $P < 0.05$). Thus, *T. longipes* and *L. sabanus* revealed an increase in above-ground movement in logged forest, whereas *M. rajah* decreased in its above-ground activity in logged forest.

Table 4. Intraspecific differences in movement trajectories between unlogged and logged forest. The two means refer to relative values from 100 m of track length in unlogged–logged forest. *Z*-values indicating significant differences for means of variables with $P < 0.05$ (Mann–Whitney *U* tests) are given in parenthesis. Positive values refer to higher averaged values for unlogged forest, whereas blank cells represent nonsignificant comparisons

	<i>Leopoldamys sabanus</i>	<i>Maxomys rajah</i>	<i>Maxomys surifer</i>	<i>Niviventer cremoriventer</i>	<i>Sundasciurus lowii</i>	<i>Tupaia longipes</i>	<i>Tupaia tana</i>	<i>Tupaia gracilis</i>
NCLIMB C2–C4	–	–	–	10–3 (2.24)	–	–	–	–
ABVGR C1	13–5 (2.11)	10–3 (2.14)	–	16–5 (2.00)	–	–	–	–
HTMOV	–	3–1 (1.98)	–	–	–	8–14 (–2.31)	–	–
MAXHT	–	0.44–0.13 (2.33)	–	–	–	–	–	–
LOGMOV	11–2 (3.35)	–	–	–	44–6 (2.00)	–	–	–
DIAM	15–6 (5.88)	–	–	–	27–10 (3.62)	15–11 (2.04)	–	27–4 (2.76)
UNDENS (1)	24–5 (2.44)	–	–	–	–	–	–	–
UNDENS (2)	68–84 (–2.56)	–	–	–	–	–	79–69 (2.24)	–
UNDENS (3)	–	–	–	–	–	–	16–25 (–2.09)	–
STEPL	2.2–1.7 (6.90)	–	1.5–1.9 (–3.51)	–	–	2.3–1.9 (4.33)	1.7–2.1 (–6.57)	–
TANGL	49–44 (–3.46)	–	–	–	–	–	–	–

Both *L. sabanus* and *S. lowii* moved longer distances on logs in unlogged than in logged forest (LOGMOV, both Mann–Whitney U test $P < 0.05$). The diameter of supportive structures used by *L. sabanus*, *T. longipes*, *T. gracilis* and *S. lowii* were larger in unlogged forest (DIAM, for all Mann–Whitney U test $U > 24.0$, $P < 0.05$) and marginally larger for all other species in logged than in unlogged forest. *L. sabanus* moved greater distances in regions with light undergrowth and shorter distances in intermediate undergrowth areas in unlogged forest (UNDENS, both Mann–Whitney U tests $U > 170$, $P < 0.05$). *T. tana* moved longer distances in areas with intermediate undergrowth but shorter distances in dense undergrowth in unlogged than in logged forest (UNDENS, both Mann–Whitney U tests $U > 286$, $P < 0.05$). Step lengths were shorter for *L. sabanus* and *T. longipes* in logged forests, whereas step lengths were longer for *M. surifer* and *T. tana* in logged forest (STEPL, all Mann–Whitney U tests $U > 196,291$, $P < 0.01$). Absolute turning angles between steps were smaller for *L. sabanus* in logged forest (TANGL, Mann–Whitney U test, $U = 206,593$, $P < 0.01$). However, despite these differences in path properties, we found no differences in the frequency distributions of step lengths (all Student's t -test $-0.55 < t_{v \geq 88} < 0.80$, $P > 0.20$) or path tortuosity (D/L, all Kruskal–Wallis ANOVA $P > 0.12$) among forest types for any of the five most intensively tracked species.

Analysis of differences of variable means between species and population of the five most intensively studied species in unlogged and logged forest by PCA (eigenvalues: $\lambda_1 = 8.68$, $\lambda_2 = 4.52$, Fig. 5) confirmed that all species changed their movement patterns, whereby the changes were most obvious for *L. sabanus*. Notably, the directions of changes in the resulting multivariate space were opposite for the species pairs *T. longipes* and *T. tana* as well as for *M. rajah* and *M. surifer* (Fig. 5).

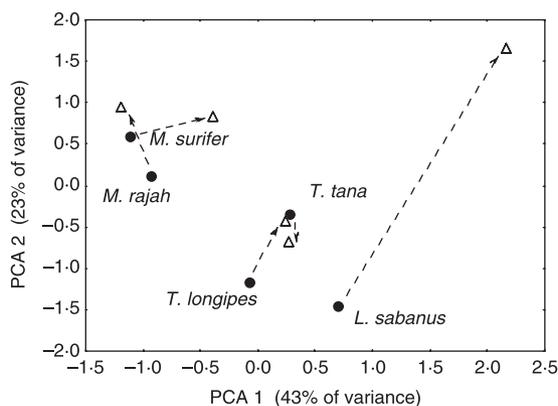


Fig. 5. Principal components analysis plot of movement trajectories of the five most intensively tracked species in unlogged (closed circles) and logged (open triangles) forest based on the means of variables. Arrows indicate the direction of changes in movement patterns in multivariate space between unlogged and logged forest. The first axis is mainly explained by MAXHT, ABVGR C2, C3 and HTMOV, whereas axis 2 is mainly described by LOGMOV, NCLIMB C1, and TANGL. Eigenvalues: $\lambda_1 = 8.68$, $\lambda_2 = 4.52$.

Discussion

INTERSPECIFIC VARIATIONS IN MOVEMENT TRAJECTORIES

The segregation of small mammals in tropical assemblages along vertical strata and/or by body size is considered to favour coexistence in species-rich communities (e.g. Charles-Dominique *et al.* 1981; Janson & Emmons 1991; Malcolm 1995; Voss & Emmons 1996; Bakker & Kelt 2000; Cunha & Vieira 2002). Although most studies have been conducted up to now in the neotropics and less is known about small mammal assemblages in the forests of South-east Asia, similar patterns in substrate use have been suggested for the neo- and the palaeotropics because of general constraints in climbing ability and adaptations to the arboreal/scansorial habitat (Emmons 1995).

Our results demonstrate that small Bornean mammals, which are mostly characterized as terrestrial/scansorial, differ in their movement trajectories with regard to several structural habitat features. Conversely, we found no differences in structural path properties that might indicate differences in movement patterns of species that differ in habitat use or morphometric features, despite the increase in step lengths with body size. Our results contrast with a study on small-scale movement strategies of American martens that were associated with structural features (Nams & Burgeois 2004). The small-scale movement pattern should differ from movements on larger scales as a response to resource distribution, which might more likely represent large-scale effects of habitat variability (e.g. Johnson *et al.* 2002; Ramos-Fernández *et al.* 2004; Solé *et al.* 2005).

Overall, our results revealed for the local assemblages on Borneo five groups of small mammals in relation to habitat use: (1) terrestrial species (*M. rajah*, *M. surifer*); (2) species that were mostly active on the ground but occasionally reached the upper canopy (*L. sabanus*); (3) terrestrial species with frequent scansorial activity (*T. tana*, *T. longipes*); (4) scansorial species that were not active in the canopy (*T. gracilis*, *S. lowii*); and, finally (5) arboreal species that occasionally approached the ground (*N. cremoriventer*, *T. minor*). We confirmed occasional arboreal activity of *L. sabanus*, although this species spends proportionally much more time on the ground than the scansorial species *S. lowii* and *T. gracilis*.

The general activity patterns were similar to those noted for mammal assemblages in the neotropics (see Charles-Dominique *et al.* 1981; Voss & Emmons 1996; Cunha & Vieira 2002). However, in contrast to studies at neotropical sites, climbing activity of small mammals was not related to body size but rather to morphometric measures (HF/HB and T/HB), indicating that species of variable sizes are adapted to cursorial vs. arboreal activity. Although some convergences of small mammals have been reported for neo- and palaeotropical assemblages (see Emmons 1995), patterns in body-size distribution cannot necessarily be expected to be equivalent. It has been

suggested that arboreal vertebrates in the neotropics are in general smaller than palaeotropical vertebrates because canopy structure is reported to be more fragile in the neotropics (Cristoffer 1987). Differences in morphological modifications such as gliding that occurs predominantly in the palaeotropics or prehensile tails that are prevalent in the neotropics may in turn affect accessibility and use of vegetation structures (Emmons & Gentry 1983). On the other hand, studies on neotropical assemblages of small mammals that contained only few species usually included also some larger bodied, mostly terrestrial didelphids, such as *Didelphis* spp. or *Metachirus* spp. (body mass > 500 g and 1 kg, respectively; references above) that might have biased the conclusions on body size distribution drawn from these assemblages.

Interestingly, habitat segregation was weak between the two species pairs based on similarities in morphology: *Maxomys rajah* and *M. surifer* as well as *T. longipes* and *T. tana*. However, as both species pairs exhibit paraphyletic relationships (Ruedas & Kirsch 1997; Han, Sheldon & Stuebing 2000), similarities in morphological appearance and body size represent convergent adaptations to their similar life styles and ecological niches. In contrast, the two smaller treeshrews *T. gracilis* and *T. minor*, which also exhibited substantial convergence in body size and morphology (Han *et al.* 2000), used distinct habitats along the vertical axis. Whereas *T. gracilis* was confined to the scansorial layer, *T. minor* was active in the upper canopy with occasional descents to the ground.

The two larger treeshrews *T. longipes* and *T. tana*, which have been mainly described as terrestrial based on field observations (Emmons 2000) and morphological traits (Sargis 2001), revealed greater climbing activity than terrestrial spiny rats, with half of all of their tracks reaching heights of 1 m or higher. Although both species were similar with regard to their movement trajectories, the higher scansorial activity of *T. tana* was not expected because it had been reported to actively dig in the leaf litter and soil for foraging, whereas the prey of *T. longipes* is probably located more on the surface of the forest floor (Emmons 2000). Therefore, with regard to our findings, orientated movement and foraging of these species may take place in different microhabitats and utilization of resource patches and interpatch movement may be independent of each other.

If rain forest mammals partition resources along the vertical axis, the finding that closely related species share a similar habitat is of much interest. The described patterns demonstrate that many factors determine assemblage structure and resource partitioning, where morphological characteristics are as important as further unknown factors, such as possible energetic constraints along the vertical axis. Further, if habitat heterogeneity and scaling effects differ between different strata, we would expect more pronounced effects of vertical habitat partitioning on the overall movement strategy contrary to our results on this single investigated scale of orientated paths.

MOVEMENT PATTERNS IN LOGGED VS. UNLOGGED FOREST

One reason that species occur in particular sets of habitats is that they are adapted to specific ecological conditions. Therefore, the potential of a species to cope with environmental variability is an important determinant in species distribution from a local to regional scale and throughout its geographical range, particularly in the heterogeneous rain forest environment. We found little evidence that any of the investigated species was restricted to a single set of habitat type and structure. Our comparisons of movement trajectories of small mammals between logged and unlogged forests clearly showed that highly modified forest structures in logged forests affected the movement trajectories of all species. The observed shifts in movement trajectories might result from the altered structure *per se*, changes in vertical partitioning of resources (e.g. Cunha & Vieira 2002) or differences in spatial orientation and environmental perception by the respective species because of the altered habitat structure (e.g. Grobety & Schenk 1992; Jacobs & Shiflett 1999). Contrary to our expectations, we found no evidence that pathways were adjusted to possible shifts in habitat heterogeneity and variability, as overall movement strategies were found to be similar in logged and unlogged forests. This weak effect of physical habitat differentiation on pathway structures reinforces the conclusion of a rather fixed movement strategy for the examined scale, as we found no differences across species or populations in different forest types.

As the response of individual species to habitat alteration was very variable, the effects of changes in habitat structure on small mammal assemblages are difficult to interpret when only single species are examined. Our results show convincingly that one needs to address the entire set of focal species for a given habitat type to reach a valid conclusion. Some general shifts in habitat use become evident when we consider the most drastic habitat change with regard to disturbance, here the reduction of canopy space and structure caused by the extraction of emergent trees in logged forests. As a consequence, arboreal species and biomass may shift from the canopy to the ground in logged forests (Malcolm 1997; Struhsaker 1997). Furthermore, differences in branch dimension and structure may alter connectivity and thus movement tracks of animals (Malcolm 1995). The predicted shifts in vertical movement patterns in response to habitat differences between understorey and canopy of logged vs. unlogged forest were less evident as we encountered terrestrial and scansorial species in logged forest with denser undergrowth and a higher variety of supportive structures at almost equal proportions. Probably, species might quickly change between two neighbouring habitat layers (here ground vs. understorey supports) and habitat differences such as microclimate between these layers might affect the species less than expected, leading to a continuous

gradient in habitat use rather than a strict terrestrial–arboreal dichotomy.

A general difference of movement trajectories between the two habitat types was only found for the diameter of supportive structures, which declined in logged forests. It needs to be noted that this general pattern refers to an overall difference in branch diameters rather than to particular preferences of small mammals for particular supportive structures. There were, for example, fewer large logs or thick arboreal branches in logged forests, whereas the abundance of thin supports increased in the understorey particularly because of the fast growing and highly abundant climbing bamboo with diameters between 1 and 3 cm that is frequently used for climbing by various species of small mammals (pers. obs.). Smaller climbing mammals might profit from thin supports because of less body mass (Lemelin 1999; Cunha & Vieira 2002), although Charles-Dominique *et al.* (1981) did not find a relationship between the diameter of supports and body sizes in an assemblage of mammals in the neotropics. However, the potential consequences of thinner supports in logged forests for individual species or the entire assemblage remain unclear. For example, *L. sabanus*, the largest focal species, frequently used thin supports (*c.* 20% of used supports = 2 cm) and showed increased climbing activity in logged forests, whereas the climbing activity of the much smaller *N. cremoriventer* was reduced in logged forests, although this species showed in general a clear preference for small diameters (Table 3). This observed variability might not be independent of other features, such as texture or the interconnectivity of supports. No general trend was found for the proportion of movements in dense undergrowth, although all species faced denser undergrowth in logged forests. Only *T. tana* and *L. sabanus* moved longer distances in dense undergrowth in logged forests. Diurnal treeshrews might profit from dense ground cover as a strategy for predator avoidance (Emmons 2000) as they generally move greater distances in dense undergrowth than nocturnal rats. Although this strategy has been suggested for several tropical small mammals (e.g. Emmons 2000; Lambert & Adler 2000; Vernes 2003) it needs to be tested with behavioural experiments and with further information with respect to associated structural, abiotic and biotic habitat features. Little is known about such differences between logged and unlogged forests. Studies comparing small mammals in undisturbed forests and tree-fall gaps therein indicate that various factors such as resource availability or protection from predators may differ in their impact on syntopic small mammals and the pay-off for them to move in densely covered gaps (Beck *et al.* 2004).

The arguments so far led us to the conclusion that any particular habitat change such as structural differences between logged and unlogged forests is closely linked to other habitat variables that might have either synergistic or reciprocal effects on small mammal movement, depending on the specific combination of

intrinsic and environmental factors. Therefore, changes in movement trajectories between forest habitats must be analysed in a multivariate approach. Our analysis suggests that specific movement patterns differ between logged and unlogged forest whereby variables related to climbing activity play a dominant role (see Fig. 5). We did not detect any trends in shifts of movement patterns with regard to body size, taxonomic grouping or vertical stratification. Further, no parallel trends were seen in the shift of movement trajectories for congeneric species pairs such as *M. rajah* and *M. surifer* or *T. longipes* and *T. tana* despite their strong convergence in morphology and habitat use.

These results highlight the importance of qualitative habitat alterations and their impact on small forest-dwelling mammals. Fortunately, most of the common species such as those in our study were able to persist in logged forest habitats. However, preliminary data from our study as well as other studies suggest that more specialized species that are rare in logged forest react negatively to environmental variability (e.g. Henein, Wegner & Merriam 1998; Purvis *et al.* 2000; Wells, pers. obs.). The results presented here are preliminary in that neither the ultimate reasons for changes in movement trajectories nor the consequences for foraging success, individual survival and population establishment can be given because of the lack of knowledge regarding the ecology of the species, in particular the rarer ones. However, first data on how species react in their movement patterns to habitat disturbance provide a promising approach for a better understanding of interspecific variation in adaptability to altered ecological conditions, determining decline or persistence of tropical rain forest mammals in local assemblages. The observed inconsistency in the species' responses to logging cautions the approach to extrapolate results obtained from a few species to a whole assemblage, underlining the importance of species-based approaches in understanding the effects of habitat degradation on speciose assemblages.

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