
Impacts of rainforest logging on non-volant small mammal assemblages in Borneo



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Summary

In the study of species-rich tropical rainforests, a central theme focuses on factors that determine diversity and patterns of species assemblages. In this context, the role of local versus regional patterns of species richness in tropical assemblages is little understood (see Condit *et al.* 2002; Hill & Hamer 2004). Because of the importance of environmental variation in organizing animal communities and populations (Kneitel & Chase 2004), the large variability inherent to undisturbed rainforests provides a wide range of challenges and opportunities for basic research approaches at the same time. In heterogeneous landscapes, organisms are not evenly distributed. Habitat selection combined with uneven resource availability in space and time leads to clumped distributions of animals in relation to favourable habitat patches (e.g. Morris 2003; Morales *et al.* 2004). In terms of basic and applied conservation research, it is important to understand not only how species are organised in species-rich assemblages in undisturbed forests, but also how conversion and loss of undisturbed rainforest affects those assemblages.

In this context, with a better understanding how and to which degree animals are linked to certain features of pristine forests and how they respond to patch dynamics, we may be able to predict their responses to habitat conversion such as logging. In return, by understanding effects of logging on species assemblages, the impact of environmental variation in structuring natural assemblages may become more apparent.

A framework for examining the effects of environmental variability on the structure and organisation of animal communities is given by the spacing and diversity of tropical trees, as they comprise the most fundamental structuring and resource-providing component of the ecosystem. For example, more than 3,000 tree species (with up to 300 species accumulating on a single hectare) have been recorded for the rainforests in Borneo, one of the 'hot spot' areas in terms of biodiversity (MacKinnon 1996; Myers 2000). Markedly, the Borneo lowlands ecoregion contain more vascular plant species than any other ecoregion on earth with approximately 10,000 species (Kier *et al.* 2005). The high diversity of trees is composed of a range of common species with a wide and rather even distribution accompanied by trees that occur at low densities and with a scattered distribution. Many trees, especially rare species, are not evenly distributed but spatially aggregated (Condit *et al.* 2000). Additionally, rainforests are frequently perturbed by local

disturbances, such as treefalls that briefly interrupt the closed canopy and homogenous forest face (Denslow 1995; Schnitzer & Carson 2001). Including those natural disturbances, diverse tropical forests are made up of patches at different successional stages, ranging from recent treefall gaps covered with pioneer vegetation to closed old-growth stands of trees (Hubbell *et al.* 1999; Molino & Sabatier 2001). Given the high diversity of trees in tropical forests, we expect to find adaptations to this ecological variability among animals that are common and widespread. In comparison, we expect to find specializations of animals on particular, patchily distributed resources among less common, locally aggregated species.

Logging of a tropical rainforest inevitably changes the composition of its flora and fauna. Whereas selective logging of commercially valuable trees may mimic numerous natural treefalls, extensive logging with clear-cutting of areas disrupts the original forest structure. In partially logged forests, old-growth trees are largely replaced by pioneering trees and other fast-growing plants. Overall, logging affects distribution and availability of resources as well as structural components of the forests. Consequently, the response of wildlife to those changes caused by logging depends on the extent of logging, forest age, and the type of animal species in question (Uutera *et al.* 2000; DeWalt *et al.* 2003). Features of logged forest differ with logging practice (e.g. conventional techniques versus lower impact techniques). With time, some ecosystem characteristics of previously logged forests may eventually converge to old-growth forest patterns (see Sist *et al.* 2003). Generally, secondary forests that have not been clear-cut may feature disturbance regimes similar to primary forest, but mostly on a much larger scale, that is with many more gaps per area than in undisturbed forests. Thus, the spatial distribution of animals in an undisturbed rainforest, particularly their use of gaps, may indicate their tolerance towards logging. Conversely, logged forests provide experimental settings that offer a broad range of different patch sizes and qualities (e.g. extent of gap features), allowing comparison of species' tolerances to contrasting environments.

Most often, logging results in a reduction of species numbers, while others do well in secondary forests (e.g. Heydon & Bulloh 1997; Malcolm & Ray 2000; Davis *et al.* 2001; Floren & Linsenmair 2001). It has, however, proven difficult to predict which species will tolerate logging at particular sites and why they do so. In logged rainforests, there is a lower survival probability for those species that are not able to cope with changes in resource availability, abiotic factors, predators, parasites, or competitors. Nevertheless, in spite of this important topic, empirical data remain rare.

Features of rainforests, such as the spatial organisation of tree species, patch sizes and characteristics or canopy stratification/percolation, are hierarchical, that is there are patches within patches (Solé & Manrubia 1995; Hubbell *et al.* 1999; Solé *et al.* 2005). Consequently, limiting factors that influence the performance of animal species may vary according to the scale of investigation (e.g. Johnson *et al.* 2002; Fritz *et al.* 2003). Logging affects not only a forest's overall architecture and resource availability, but also the degree of habitat heterogeneity (Cannon *et al.* 1998). Therefore, assessing the effects of logging depends strongly on the scale on which the analysis is conducted. Results vary also with the taxonomic group under investigation (e.g. Condit *et al.* 2002; Hill & Hamer 2004). This might be particularly true for species that are involved in multiple top-down and bottom-up processes, viz. animals that comprise important consumers of a range of plant and animal resources and, simultaneously, serve as essential prey to other ecosystem components. These species might be affected by logging either directly or via indirect effects arising from interactions with other species (Terborgh *et al.* 2001). In such species-interacting system, all involved species and levels of investigation might be subject to specific scaling effects. Hence, comparison of animal assemblages in logged and pristine forests is scale-dependent and needs to include the effects of environmental variability in order to predict differences in community structure and dynamics. To conclude, it is essential to use multifaceted approaches to appreciate the impact of logging on a particular group of species. To understand why only some species are able to persist in logged forests, we need to determine the degree of persistence and environmental interplay for each species on various scales, taking into account that multiple factors may act on different scales.

As logging activity increases in tropical rainforests, it is crucial to better understand the extent to which changes in species assemblages and species interactions with the environment affect the function of rainforest ecosystems. Currently, the most rapid deforestation and biodiversity loss occurs in the dipterocarp rainforests of southeast Asia. Three quarters of the original stands are likely to be either completely lost or converted into heavily degraded secondary forests by the end of this century (Curran *et al.* 2004; Sodhi *et al.* 2004), eliminating a huge proportion of the region's biodiversity (see Brook *et al.* 2003). In Sabah (Malaysia), northwestern Borneo, more than 90 % of the primary rainforest was already lost or converted to secondary forest between 1970 and 1996 (Sabah State Government 2001). In the rainforests of Borneo, conventional logging usually damages more than 50 % of the original stands, with extraction rates exceeding

10 trees/ha (Sist *et al.* 2003 and references therein). Soon, primary rainforests will be restricted to a limited number of conservation areas. Currently, about half (48 %) of the land surface in Sabah is covered with forests that are disturbed to various extents (WWF 2005; Sabah Forest Department, pers. comm.). However, the presence of relatively large forest remnants with various disturbance regimes and histories provides a suitable experimental setting for investigating assemblages and species performances from local to regional scales, incorporating environmental heterogeneity both within and among forest types. Examining species distributions across pristine forest ecotones and following anthropogenic disturbances may thus be an effective way to understand assemblages in logged forests and to assess the conservational value of these forests.

We understand little about the impact of habitat degradation on small mammal communities and species performances. Whereas the effects of forest fragmentation on small non-volant mammal communities (e.g. Laurance 1994; Lynam & Billik 1999; Goodman & Rakotondravony 2000) and small mammal assemblages in landscapes including rainforest remnants (Gascon *et al.* 1999; Pardini 2004) are increasingly being investigated, only very few studies have addressed the effects of logging on small non-volant mammal communities in Asian tropical forests (e.g. Wu *et al.* 1996; Zubaid & Ariffin 1997; Laidlaw 2000; Yasuda *et al.* 2003; Bernard 2004) or elsewhere in the tropics (e.g. Laurance & Laurance 1996; Struhsaker 1997; Malcolm & Ray 2000; Ochoa 2000; Lambert *et al.* 2005). Generally, the studies suggest that small mammal assemblages are lower in species richness in logged forests compared to primary forests (e.g. Malcolm & Ray 2000; Lambert *et al.* 2005). Furthermore, methodological and logistic problems make studies of small mammals difficult to conduct. Most studies included only two sites, comparing disturbed versus undisturbed habitats, and few studies provide insights into the life history or spacing patterns of particular species (e.g. Liat 1970; Kawamichi & Kawamichi 1979; Emmons 2000; Wiens & Zitzmann 2003; Wells *et al.* 2004b; Meijaard *et al.* 2005; Merker *et al.* 2005).

Nevertheless, small mammals are a promising group for investigating the effects of logging, because proximate mechanisms of the decline or increase of a wide range of plant and animal species might be linked to the crucial roles of small mammals in multiple bottom-up or top-down interacting agents at various scales. The intensive use of tropical forests by ecologically highly diverse and versatile non-volant small mammal assemblages throughout the forests' three-dimensional space (Bourliere 1987; Wells *et al.* 2004a) grants mammals access and interaction with a wide array of other ecosystem components. Non-volant small mammals play a central role

in tropical forests, because many are important consumers of seeds and seedlings of trees that in turn contribute to diversity and structural richness of the forests (Struhsaker 1997; Asquith *et al.* 1997; Blate *et al.* 1998; Curran & Webb 2000). Increases in densities of some small mammal species that adapt well to secondary forests may, for example, increase seed predation and suppress forest regeneration (Struhsaker 1997). Other mammals are likely to contribute positively to forest regeneration and maintenance of diversity by dispersing seeds or preying on herbivorous invertebrates. Knowledge of the ecology of species that thrive in secondary forests is crucial as their impact upon plant regeneration is related to their consumption of specific plant material and/or of herbivorous arthropods that affects the extent and speed of regeneration. Furthermore, knowledge of movement patterns of small mammals is crucial to better understand whether they mainly exploit the ground-level forest floor or the structural-rich canopy regions. Vice versa, the availability of fruit or other plant material strongly influences and regulates small mammal populations (Adler 1998). The nutritious seeds of Dipterocarpaceae, for instance, represent a seasonally available key resource for rats and other vertebrates in southeast Asian forests (Curran & Webb 2000; Wells & Bagchi, in press). In logged forests, dipterocarps are replaced by pioneer trees with fruits of lower nutritional value to vertebrates (Curran & Webb 2000). Hence, large expanses of pioneer vegetation in logged forest is likely to change resource availability for small mammal populations, which in turn regulate growth and reproduction of a large number of plants, depending on their main diet.

Small mammals also experience top-down regulations. They are important prey items for many predators, including meat-eating mammals, birds of prey, and reptiles. These mostly large predators are particularly sensitive to anthropogenic disturbance of rainforests. Their loss influences abundances of small mammals, and consequently, the diversity of assemblages and specific interactions of species on various levels within complex, trophic cascades (Terborgh *et al.* 2001).

In addition, infections by ecto- and endoparasites also regulate population density of small mammals. The many life history and dispersion patterns exhibited by small mammals provide favourable conditions to ensure the establishment, transmission and persistence of a diverse parasite fauna. Patterns of parasitism in animal populations are largely influenced by host-specific traits such as host density, space use, ranging, contact rates, social system, and diet (Holt *et al.* 2003; Nunn *et al.* 2003). Parasites have an important influence on their hosts' life-history strategies and population demography (Dobson & Hudson 1986). Environmental changes such as

logging and stress leading to an altered environment are therefore likely to profoundly affect the fitness of the host species and of the parasites as well, depending on the host-specific traits and their susceptibility toward changes in environmental conditions and the prevalence of parasites (Lafferty & Holt 2003 and references therein). In spite of the prevalence and impact of parasites on small mammal fitness and population density (Dobson & Hudson 1986), we know very little about the effects of rainforest disturbance on parasite loads. Recent studies suggest that rainforest disturbance results in greater levels of parasitism and disease incidence in vertebrates (Ostfeld & Holt 2004; Gillespie *et al.* 2005). Research on the extent of parasitism of tropical vertebrates is still in its infancy. However, by determining infestation patterns and parasite assemblages across various hosts, we will get closer to a better understanding of the proximate mechanisms of some vertebrates' response to logging. Most importantly, in species-rich assemblages, sympatric species exhibit many different relationships regarding their taxonomy, life-history, habitat utilisation and feeding habits, which allow to unravel the influence of various small mammal traits on their associated parasite fauna. Similarities in these traits are likely to determine similarities in associated parasite assemblages (see Holt *et al.* 2003; Nunn *et al.* 2003), and a similar susceptibility of particular species towards logging may be predicted by similarities in specific traits and habitat affiliations. Host-parasite relationships therefore provide an important model system to study the effects of logging on the fitness of small mammal populations.

The overall objective of this study was to determine how non-volant small mammal assemblages are affected by rainforest logging in the dipterocarp rainforest in Borneo (Sabah, Malaysia). I approached this topic by systematically investigating various aspects of small mammal assemblages in three primary and three secondary forest sites over a period of two years.

Specifically, this study aimed at investigating the following questions:

- 1) Do diversity, species composition, and assemblage variability of small mammals differ in undisturbed and logged rainforests?
- 2) Do logging-induced habitat differences influence the habitat use and movement trajectories of common small mammal species?
- 3) What are the characteristics of movement and ranging patterns of the giant rat *Leopoldamys sabanus* in different forest types? Do these trajectories differ at different scales?
- 4) Do prevalence and richness of parasitic helminthes differ in common small mammals? Are these helminth assemblages affected by logging?

A key objective of this study was to determine how the diversity and population dynamics of small mammal assemblages are affected by logging, and whether these patterns can be traced down to particular species with specific ecological characteristics (**Chapter 1**). Repeated sampling in various sites aimed at shedding light onto the question whether variability in species presence and population densities - prominent either within or among forest types – might give a biased view of species persistence in logged forest if only a pair-wise site comparison is undertaken. Indeed, I found that local assemblages of small mammals differed in their species composition between primary and secondary forest when only single sites were compared, but they hardly differed in their dynamics on a larger scale. About a third of the species ($N = 11$) out of the 28 species trapped accounted for 95 % of all captures. Species richness and diversity were significantly higher in primary forest (27 species) than in secondary forest (17 species) mostly because of the lower number of rarely recorded species in secondary forest. Assemblages of rats (Muridae) and tree shrews (Tupaiaidae) showed similar population fluctuations in space and time, indicating that the ecology of these taxa may be partially driven by the same environmental factors. Species were patchily distributed within sites. The analyses at local and regional scales revealed similar patterns in diversity and assemblage variability, suggesting that the effects of forest degradation on the small mammal assemblages were not scale-dependent. These results emphasize the importance and conservation value of degraded forest stands that are able to hold a large proportion of small mammals found in undisturbed rainforests. The presence of the most common species of rats and tree shrews at all forest sites suggests that these species are tolerant toward habitat changes. The arboreal rat *Niviventer cremoriventer* and the terrestrial tree shrew *Tupaia tana* even increased in abundance in secondary forest and hence might benefit from forest degradation. However, rare and more specialized species are vulnerable to forest degradation, with the loss or decrease in abundance of certain functional or taxonomic groups, such as some arboreal small mammals and civets (Viverridae), indicating a depauperate habitat.

My second objective was to determine whether similar habitat requirements permit predictions of responses to logging among species. For this purpose, I used movement paths of animals to assess their habitat use. This allowed me to derive predictions on the effects of habitat structure and disturbance on distribution and habitat utilisation of the small mammals. I investigated movement trajectories and stratification for eight common species by spool-and-line tracking following a total of 13,525 m path (**Chapter 2**). Variables related to climbing activity of the small mammals as well as supportive structures and undergrowth density of the vegetation were

measured along the tracks of the animals. Movement trajectories differed significantly between the small mammals, with the highest degree of similarity among congeneric, similar-sized species with similar morphology. All species were affected by alterations of forest structure in secondary forest compared to pristine forest. The long-tailed giant rat *Leopoldamys sabanus* showed the greatest difference in movement paths between primary and logged forest. The diameter of supportive structures, which was smaller in secondary than in pristine forests, affected all species in a similar way. Overall, shifts in microhabitat use showed different trends among species. Two species pairs, *Maxomys rajah* and *M. surifer* as well as *Tupaia longipes* and *T. tana*, revealed opposite trends in their altered microhabitat use in secondary forest. This illustrates that each species was uniquely affected in its movement trajectories, probably caused by a unique suite of environmental and intrinsic features.

More detailed analyses of movement and ranging pattern were undertaken for the giant rat *L. sabanus* by comparing small-scale patterns obtained from spool-and-line tracks with large-scale patterns derived from nightly radio-tracking. This approach aimed at understanding whether tracking with spool-and-lines or with transmitters revealed comparable geometric path properties, and consequently, how habitat degradation affects movement patterns of giant rats at different scales (**Chapter 3**). At the small scale, paths were relatively straight. Step lengths (straight-line sections with no recognizable change in direction and no change in recorded habitat characteristics) were shorter in secondary forest than in primary forest. However, the distribution of step lengths in both forest types did not follow a normalized probability distribution, therefore rejecting random walk models, which are broadly applied as a null hypothesis in model animal movement in homogeneous landscapes (see Turchin 1998). On the larger scale (16 radio tracks of individuals of four nights each), move lengths during 10-min intervals, where the tagged animals covered mean distances of 32.09 ± 44.85 m ($N = 2,432$), were described by similar power-law distributions for logged and pristine forests and revealed significant serial correlation. These patterns also rejected the assumption of a correlated random walk but rather comprised a broad distribution of long movements interrupted by localized concentration of shorter moves similar to patterns described as Lévy walks. The minimum distance travelled per night was $1,443 \pm 991$ m during activity periods of 485 ± 109 min, resulting in nightly ranges between 535 to 8,987 m² (95 % kernel estimates). There were no common patterns at the two scales examined or the two tracking techniques applied, respectively. The large variability in movement parameters among individuals was neither predicted by sex nor forest type, suggesting that the patterns of these

paths were responses to local patches in a complex, heterogeneous rainforest environment where the animals presumably locate highly clumped resources. The similar movement patterns observed in primary and secondary forest suggest that logged forests retain many features relevant to movement and ranging patterns found in primary forest. The results also support the notion that *L. sabanus* is a generalist regarding habitat use and foraging strategy.

Finally, I examined assemblages of parasitic helminths (Nemathelminthes, Plathelminthes) in the gastrointestinal tracts of four species of rats and tree shrews in both primary and secondary forests (**Chapter 4**). Parasitic helminths are especially suited for comparing differences in parasite assemblages among species and populations in different forest types. The various transmission patterns of helminths that range from direct to indirect transmission imply different infestation patterns of their hosts, in this case small mammals, and are linked to their life history, habitat use, and feeding habits. Indirectly transmitted helminths rely on specific associations with invertebrates that serve as prey for their definitive hosts, whereas directly transmitted helminths profit from frequent encounter rates of individual host that in turn require spatial and temporal overlap in habitat use. Detection of helminths by faecal egg count allowed for non-invasive and intensive screening of four common host species with a total of 337 samples being investigated. Nematode eggs prevailed in 95 % of all samples with up to five morphotypes. Whereas members of the order Strongylida were most prevalent in *L. sabanus* and the tree shrews *Tupaia longipes* and *T. tana*, the order Spirurida dominated in *N. cremoriventer*, which revealed the lowest average nematode prevalence and egg density. Cestode eggs were only found in samples from *L. sabanus* and *T. tana*. Comparison of parasitic helminths in small mammals revealed that species richness and relative abundance of the helminths were clearly influenced by rainforest logging. However, the host species differed strongly in the direction of the infestation pattern. Species richness of nematode morphotypes and mean number of infections per host were significantly higher in secondary forest than in primary forest for *T. longipes*. In contrast, *L. sabanus* was more heavily infected with cestodes in primary than in secondary forest and also revealed larger egg counts for strongylids and spirurids in primary forest. These results suggest that forest degradation and altered environmental conditions influence helminth diversity and infestation patterns of small mammals. However, prediction of infestation patterns requires further studies, as patterns among host species were inconsistent so far.

To summarize, this study emphasises the importance of local ecological interactions and within-habitat dynamics in contributing to the spatial dynamics of small mammal assemblages in dipterocarp rainforests. The variability in spatio-temporal habitat use within local assemblages of small mammals and the large variability in individual movement patterns tended to be greater between sites than differences induced by logging, demonstrating the difficulty in predicting the effects of logging. In this regard, it is vital to pay attention to the large, scale-dependent variability in resource distribution and structure within primary and secondary rainforests. The high level of forest heterogeneity in both forest types, mainly attributable to its patchy nature and the influence of environmental factors that may vary geographically even over short distances, may help to explain the surprisingly weak effects of logging on small mammal assemblages. Caution is therefore needed in interpreting any inconsistent responses of community or species performance to habitat disturbance such as logging, as the large variability within forest types may blur adverse effects of such disturbances. It also has to be stressed that the role of rare species remains especially elusive, as the detailed behavioural data presented here stem from species that were common at all sites with similar species abundances and population fluctuations at logged and unlogged sites. The reduced species richness in logged forests clearly shows that some species are vulnerable to severe population reductions or extinction by logging-induced changes. Further, logging effects may vary with the scale of analysis, since different ecological interactions may become influential at different scales, as it is suggested by the movement and ranging patterns of giant rats. Estimating logging effects on a species or taxonomic group needs therefore to take into account that the hierarchy of habitat selection and behaviour should reproduce the hierarchy of potentially limiting factors. The inconsistent responses of several common mammal species to logging with regard to movement trajectories and composition of parasitic helminth assemblages prevent general predictions about the effects of logging on small mammals. It became clearer with this study that multiple sets of environmental and intrinsic features unique to a species determine the outcomes of logging.

To conclude, the variable interactions of small mammals with a variety of environmental factors in local patches within complex and heterogeneous environments presents a major challenge for qualitative/quantitative investigations of traits that allow species to persist in disturbed rainforests. While generalist small mammals may indeed be able to cope with altered habitat conditions, more advanced approaches are indispensable to quantify the extent of variation and habitat conversion that specialists are able to tolerate. More insights into such patterns may also

promote innovative conservation and forest management strategies where lower impact logging is applied, or where old-grown forest patches within commercially used rainforests are preserved, to preserve and restore as many small mammals as possible and thus maintain ecosystem services such as seed dispersal and predation of herbivorous insects.

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Zusammenfassung

Habitatdegradation durch anthropogenen Wandel der tropischen Regenwälder bewirkt eine zunehmende Gefährdung und Reduktion von Wildtierpopulationen. Effektive Schutzmaßnahmen erfordern Untersuchungen, die erklären, warum sich nur bestimmte Arten an sekundäre Habitate anpassen können und welche Verbreitungsmuster von Tiergemeinschaften in gestörten Waldsystemen daraus resultieren. Ein näheres Verständnis dieser Zusammenhänge ist sowohl für die Grundlagenforschung als auch für die Naturschutzbiologie von großer Bedeutung. Hierbei fehlt jedoch nicht nur weitgehend das Wissen, wie stabil oder dynamisch die Gemeinschaften in natürlichen Waldökosystemen sind, sondern auch, wie diese auf großflächige Habitatumwandlung und -degradation durch anthropogene Einflüsse reagieren. Großflächige Abholzungen („Logging“) stellen dabei eine vielfache Verstärkung der dem ursprünglichen Regenwald intrinsischen Variabilität und Heterogenität dar, wie sie sich z.B. in der Bestandslückendynamik manifestiert. Die daraus resultierenden Mosaikstrukturen sowie hierarchisch gegliederte Habitateigenschaften (d.h. Mosaikstrukturen innerhalb bestehender Mosaike von z.B. Baumkronenstrukturen) lassen je nach spezifischen ökologischen Anforderungen (Eurypotenz) und Dispersionspotential charakteristische Verteilungsmuster unterschiedlicher Arten innerhalb von Tiergemeinschaften erwarten. Die Bedeutung verschiedener limitierender Faktoren, die die Fitness von Arten beeinflussen, variiert dabei auf unterschiedlichen Skalenebenen, wodurch die Bewertung des Einflusses von Abholzungen auf Tiergemeinschaften je nach Betrachtungsebene ein unterschiedliches Ergebnis liefern kann. So kann z.B. das lokale Ressourcenangebot (z.B. ein fruchtender Baum) das lokale Artvorkommen (des Fruchtkonsumenten) kurzfristig bestimmen, während regulierende Mechanismen wie der Einfluss von Predatoren auf regionaler Ebene längerfristig auf die Populationsgröße (des Fruchtkonsumenten) einwirken. Entsprechend gewinnt in den Untersuchungen von ausgewählten Taxa in gestörten Regenwäldern die Berücksichtigung von Skaleneffekten und von 'top-down' oder 'bottom-up' regulierenden Mechanismen zunehmend an Bedeutung.

In diesem Zusammenhang stellen tropische Kleinsäugergemeinschaften, die bisher nur wenig untersucht wurden, ein besonders vielversprechendes Modell dar, um die Auswirkung von Abholzungen auf Tiergemeinschaften zu untersuchen. Kleinsäuger sind in tropischen

Regenwäldern in abundanten und diversen Gemeinschaften anzutreffen, die den gesamten dreidimensionalen Raum bewohnen. Die überwiegend omnivore Ernährungsweise vieler Arten umfasst eine breite Palette verschiedener Früchte/Samen sowie anderer Pflanzenteile, Invertebraten und kleinerer Vertebraten. Weiterhin sind Kleinsäuger eine wichtige Nahrungsquelle für karnivore Großsäuger und zudem ein vielseitiges Habitat für eine diverse Parasitenfauna. Diese multilateralen Einbindungen in komplexe trophische Kaskaden sowie die zahlreichen unterschiedlichen taxonomischen und funktionalen Beziehungen von sympatrischen Arten innerhalb einer Gemeinschaft erlauben vielseitige vergleichende Untersuchungsansätze, wie Habitatdegradation sich auf Arten mit unterschiedlichen ökologischen Ansprüchen und Morphologie auswirken kann.

In der vorliegenden Arbeit untersuchte ich anhand sympatrischer Kleinsäugerarten im Regenwald von Borneo (Sabah, Malaysia), wie Habitatdegradation sich auf populationsdynamische Prozesse und die spezifische Raumnutzung sympatrischer Arten auswirkt. Hierzu bearbeitete ich über ein Zeitraum von zwei Jahren in drei Primär- und drei Sekundärwälder verschiedene Aspekte mit folgenden Fragestellungen:

- 1) Wie wird die Diversität, Artenzusammensetzung und Populationsdynamik von Kleinsäufern durch Habitatveränderung und –degradation beeinflusst?
- 2) Wie unterscheiden sich häufige Kleinsäugerarten in ihrer Habitatnutzung und Fortbewegungsweise zwischen gestörten und ungestörten Waldgebieten?
- 3) Wie sieht die Fortbewegungsweise und die Aktionsraumgröße der Langschwänzigen Riesenratte *Leopoldamys sabanus* in gestörten und ungestörten Waldgebieten aus und wie stark werden diese Charakteristika durch die Betrachtung auf zwei Skalenebenen (groß- und kleinräumig) beeinflusst?
- 4) Worin unterscheidet sich die parasitische Helminthenfauna ausgewählter Kleinsäugerarten und wird diese durch Regenwalddegradation in ihrer Diversität und Zusammensetzung beeinflusst?

Die mit mehreren Replika durchgeführten Untersuchungen in unterschiedlichen Waldgebieten dienten dabei als Grundlage, um herauszufinden, ob die bisher postulierte Variabilität lokaler Kleinsäugergemeinschaften innerhalb und zwischen unterschiedlichen Waldtypen vorwiegend darauf zurückzuführen ist, dass die meisten der bisherigen Studien nur paarweise durchgeführt wurden, das heißt ohne Replikas der jeweiligen Habitate. So konnte ich anhand meiner Daten zeigen, dass paarweise Vergleiche der lokalen Gemeinschaftszusammensetzungen deutliche

Unterschiede zwischen Primär- und Sekundärwald aufwiesen, dass jedoch Analysen, die ich über den gesamten Stichprobenumfang hinweg durchführte, keine deutlichen Unterschiede in den Gemeinschaften zeigten (**Kapitel 1**). Weder in den Populationsschwankungen der häufigen Arten noch in der Gemeinschaftszusammensetzung fand ich signifikante Unterschiede zwischen den beiden Waldtypen. Insgesamt dokumentierte ich 28 Arten für die Kleinsäugergemeinschaft, wobei etwa ein Drittel der Arten ($N = 11$) 95 % aller Fänge ausmachten. Artenreichtum und Diversität der Gemeinschaften waren signifikant größer im Primärwald (27 Arten) im Vergleich zum Sekundärwald (17 Arten), wo weniger der selten nachgewiesenen Arten gefangen wurden. Lokale Gemeinschaften von Ratten (Muridae) und Spitzhörnchen (Tupaiidae) fluktuieren dabei ähnlich in ihrer Zusammensetzung und relativen Abundanz einzelner Arten in Raum und Zeit, was darauf schließen lässt, dass vergleichbare ökologische Faktoren auf beide Taxa einwirken. Einige Arten wiesen ein geklumpstes Vorkommen innerhalb der Waldgebiete auf. Die Ähnlichkeit der Ergebnisse der Diversitätsuntersuchungen auf lokaler und regionaler Ebene deutet allerdings darauf hin, dass Ergebnisse bezüglich der Artenzusammensetzung und Gemeinschaftsdynamik nicht notwendigerweise skalenabhängig sind. Die Ergebnisse betonen neben der wichtigen Bedeutung von Primärwaldgebieten die Schutzwürdigkeit gestörter Regenwaldhabitate und deren Bedeutung für den Naturschutz, insbesondere, da ein Großteil der im Primärregenwald heimischen Kleinsäugerfauna mit ähnlichen demographischen Merkmalen auch im gestörten Waldhabitat präsent ist. Allerdings deutet die reduzierte Anzahl von vorwiegend seltenen und relativ spezialisierten Kleinsäugerarten im Sekundärwald auch darauf hin, dass gestörte Regenwälder nur beschränkt die Funktion von ursprünglichen Wäldern ausüben können und die Dezimierung des Lebensraums mit einem Artenschwund bestimmter funktionaler oder taxonomischer Gruppen von Kleinsäufern wie z.B. arborealen Arten oder Schleichkatzen (Viverridae) einhergeht.

Ein vorwiegend euryökes Verhalten und eine entsprechende Toleranz gegenüber Habitatdegradation fand ich für die häufigen Ratten- und Spitzhörnchenarten, da diese alle in den unterschiedlichen Waldgebieten vorkamen. Hier stellte sich die Frage, inwieweit sympatrische Arten in ihrer Habitatnutzung überlappen und gemeinsame Merkmale bestimmter Arten eine Voraussage über die artspezifische Reaktion auf Lebensraumveränderungen zulassen.

Viele Habitateigenschaften und auch die Reaktionen einer Art auf lokale Bedingungen spiegeln sich in ihrer Fortbewegungsweise wider. Die Analyse von Bewegungs- und Fouragierverhalten sollte daher einen weiteren Einblick erlauben, wie sich veränderte Bedingungen im Sekundärwald auf das Vorkommen und die Verteilung von Kleinsäufern auswirken. Ein weiteres

Ziel dieser Arbeit war daher der Vergleich von Habitatnutzung und Fortbewegungsweise von acht häufigen Kleinsäugerarten durch die Analyse von insgesamt 13.525 m Wegstrecke, die mit Hilfe einer Fadenspulvorrichtung gewonnen wurde (**Kapitel 2**). Hierzu nahm ich verschiedene Variablen der jeweiligen Lebensräume wie z.B. Typ und Dichte des Unterwuchs, Durchmesser der von den Kleinsäufern genutzten Strukturen und die Kletteraktivität der markierten Tiere entlang der Wegstrecke auf. Die Wegstrecken unterschieden sich deutlich zwischen allen untersuchten Arten, wobei die größten Übereinstimmungen zwischen Arten mit sehr ähnlicher Morphologie und Körpergröße festzustellen waren. Alle Arten wurden in ihrer Fortbewegungsweise durch Habitatdegradation beeinflusst. Die deutlichsten Unterschiede fand ich bei der Riesenratte *L. sabanus*. Die Durchmesser genutzter Strukturen, die im Sekundärwald geringer waren als im Primärwald, stellten die einzige Variable dar, die sich für alle untersuchten Arten im Sekundärwald gleichermaßen änderte. Bezüglich der veränderten Wegstrecken fand ich jedoch kein einheitliches Muster, vielmehr konnten gegenläufige Reaktionen auf Habitatveränderungen für die konvergenten Artenpaare *Maxomys rajah* und *M. surifer* sowie für *Tupaia longipes* und *T. tana* festgestellt werden. Ich schloss daraus, dass Arten somit in ihrer Fortbewegungsweise durch spezifische und multiple Kombinationen von Habitateigenschaften und artspezifischen Merkmalen beeinflusst wurden.

Eine detailliertere Analyse der Fortbewegungsweise und Raumnutzung nahm ich für die Riesenratte *L. sabanus* auf zwei unterschiedlichen Ebenen durch die Anwendung der Fadenspultechnik und Radiotelemetrie vor (**Kapitel 3**). Dabei ging ich der Frage nach, ob die mit zwei Methoden auf unterschiedlichen Ebenen untersuchte Fortbewegungsweise durch gleiche geometrische Eigenschaften gekennzeichnet war und inwieweit diese durch Habitatänderungen beeinflusst wurden. Kleinräumige Wegstrecken, die mit Hilfe der Fadenspulvorrichtung analysiert wurden, verliefen dabei relativ geradlinig und zielgerichtet. Die Schrittlängen (Teilabschnitte ohne sichtbaren Richtungswechsel) der Riesenratte waren signifikant kürzer im Sekundär- als im Primärwald, wobei jedoch die Größenverteilung der Schrittlängen für beide Waldtypen sehr ähnlich war. Die Größenverteilungen war nicht normal verteilt, so dass eine der Grundvoraussetzungen für die vielfach angewendeten Modelle der Zufallsbewegungen im Raum, der sog. ‚Random walks‘, nicht erfüllt war. Die Verteilungen der zurückgelegten Distanzen innerhalb von 10-Minuten-Intervallen (Telemetriedaten) waren dagegen für beide Waldtypen durch ähnliche Power-law Anpassungen (Potenz- bzw. polynomiale Beziehungen zwischen Häufigkeit und Länge von zurückgelegten Distanzen) gekennzeichnet. Die seriell korrelierten

Distanzlängen deuteten darauf hin, dass z.B. aufeinanderfolgend mehrmals relativ kurze Distanzen zurückgelegt wurden. Diese Muster entsprachen einer Lévy-Verteilung und unterschieden sich somit ebenfalls von klassischen Random walks. Die gesamte mittlere nächtliche Laufstrecke der Riesenratten betrug 1.443 ± 991 m, die in Aktivitätsperioden von 485 ± 109 min zurückgelegt wurden und in Aktionsraumgrößen von 535 bis 8.987 m^2 (95 % Kernel-Abschätzungen) resultierten. Die mit zwei Methoden auf zwei Ebenen analysierten Fortbewegungsweisen der Riesenratten ließen wenig gemeinsame Muster erkennen. Die relativ große Variabilität der bezüglich Fortbewegung und Raumnutzung gemessenen Parameter zeigte keinen Zusammenhang mit dem Waldtyp oder dem Geschlecht der Tiere, vielmehr ist sie wahrscheinlich als lokale Antwort auf lokale Bedingungen in dem hochvariablen und heterogenen Ökosystem der tropischen Wälder zu sehen. Ich schliesse aus meinen Ergebnissen, dass gestörte Waldsysteme viele Eigenschaften der Primärwälder beibehalten, die die Fortbewegungsweise von häufigen Kleinsäugerarten wie *L. sabanus* beeinflussen.

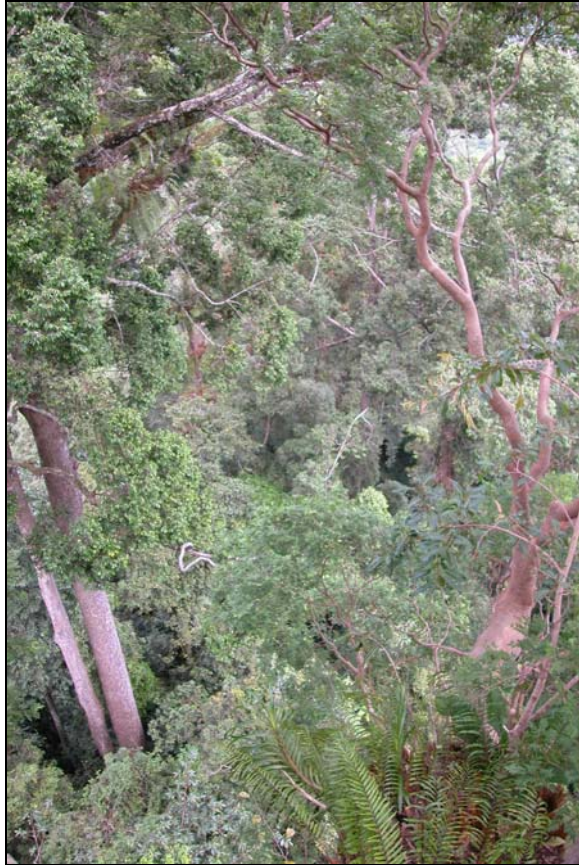
Abschließend habe ich die gastrointestinale Helminthenfauna (Nemathelminthes, Plathelminthes) von vier häufigen Kleinsäugerarten in Primär- und Sekundärwäldern untersucht (**Kapitel 4**). Parasitische Helminthen sind ein besonders geeignetes Modell, um Unterschiede in der Parasitierung verschiedener Arten oder Populationen zu vergleichen. Die unterschiedlichen direkten und indirekten Übertragungswege führen zu unterschiedlichen Zusammensetzungen der Helminthen in den einzelnen Wirtsarten und -populationen, wobei Lebensgeschichte, Habitatnutzung, Fortbewegung und Nahrung der Wirte wichtige Determinanten sind, welche die Infektionsraten beeinflussen. Während indirekt übertragene Helminthen die Interaktion mit bestimmten Invertebraten erfordern, die vom entsprechenden Kleinsäugerwirt gefressen werden müssen, wird die Transmission von direkt übertragenen Helminthen durch häufige Kontakte unterschiedlicher Wirtstiere und deren Überlappung in ihrer Raumnutzung begünstigt. Ein Vergleich der Unterschiede in den Parasitierungsraten und -zusammensetzungen von Kleinsäugerarten und -populationen in Primär- und Sekundärwäldern sollte daher interessante Rückschlüsse erlauben, wie Habitatveränderungen sich auf die Ressourcen- oder Habitatnutzung dieser Kleinsäuger auswirkt. Die Wurmei- bzw. Oocystenzählung (McMaster-Verfahren) ermöglichte mir eine intensive und nichtinvasive Untersuchung von vier Kleinsäugerarten mit insgesamt 337 analysierten Proben. Ich fand Nematodeneier in 95 % aller Proben, wobei bis zu fünf Morphotypen pro Wirtstier vorkamen. Die Ordnung Strongylida dominierte in *L. sabanus* und den Spitzhörnchen *T. longipes* und *T. tana*, während die Ordnung Spirurida als Haupttaxon in

N. cremoriventer vorkam. *N. cremoriventer* wies die geringste Anzahl an Infektionen und die niedrigste Wurmeidichte im Kot auf. Cestodeneier wurden nur für *L. sabanus* und *T. tana* nachgewiesen. Die Parasitengemeinschaften der untersuchten Kleinsäugerarten wurden eindeutig durch Habitatdegradation beeinflusst. Die Anzahl an unterschiedlichen Morphotypen und die Infektionsrate von *T. longipes* war signifikant höher in Sekundär- als in Primärwäldern. Dem gegenüber wies *L. sabanus* eine höhere Infektionsrate mit Cestoden und höhere Befallsintensitäten mit Eiern von Strongyliden und Spiruriden im Primär- als im Sekundärwald auf. Die Änderungen in den Parasitengemeinschaften im gestörten Waldsystem zeigten somit keine einstimmigen Muster zwischen Kleinsäugerarten und bestätigten, dass sich Habitatdegradation unterschiedlich auf verschiedene Wirtsarten auswirken kann. Diese Befunde stimmten daher auch mit meinen Ergebnissen zur artspezifischen Habitatnutzung und Fortbewegungsweise von Kleinsäufern im Vergleich von Primär- zu Sekundärwäldern überein, die ebenfalls kein einheitliches Bild aufwiesen.

Fazit und Ausblick. Zusammenfassend zeigt meine Arbeit, dass lokale ökologische Interaktionen und habitatinterne Variabilität/ Mosaikstruktur wichtige Faktoren sind, die zur räumlich-zeitlichen Dynamik und der heterogenen Strukturierung von Kleinsäugergemeinschaften im asiatischen Regenwald beitragen. Sowohl die räumlich-zeitliche Struktur lokaler Kleinsäugergemeinschaften, sowie die gefundenen lokalen Muster im Fortbewegungsverhalten der Riesenratte *L. sabanus* wiesen eine hohe Variabilität auf, die meiner Ansicht nach zum Teil mögliche Unterschiede zwischen Primär- und Sekundärwäldern weitgehend nivellierte. Daraus ergab sich, dass die Auswirkungen von Habitatdegradation nur schwach oder zum Teil nicht eindeutig sichtbar wurden. In diesem Zusammenhang ist hervorzuheben, dass die unerwartet schwachen Auswirkungen der Habitatdegradation wahrscheinlich im engen Zusammenhang mit der hohen Variabilität der Ressourcenverteilung und Habitatstruktur innerhalb der Primärwälder im Vergleich zu den Sekundärwäldern stehen. Besondere Vorsicht ist deshalb bei allgemeingültigen Aussagen geboten, die auf einen kleinen Datensatz untersuchter Gebiete oder Arten beruhen, da die in primären Regenwäldern intrinsisch hohe Variabilität nachteilige Auswirkungen der Regenwaldzerstörung weitgehend überlagern. Da die vorliegenden Ergebnisse an verhältnismässig häufigen, zumeist generalistisch ausgerichteten Kleinsäugerarten gewonnen wurden, bleibt die Auswirkung von Habitatdegradation auf die seltene Kleinsäugerarten offen. Hierbei sind andere Ergebnisse zu erwarten, da der beobachtete Artenschwund im Sekundärwald darauf hinweist, dass einzelne Arten wesentlich sensibler auf anthropogene Habitatdegradation

reagieren und mit zunehmender Regenwaldkonversion in ihrem Bestand gefährdet sind. Weiterhin weisen die Unterschiede in der Fortbewegungsweise und der Aktionsraumnutzung von *L. sabanus* im Vergleich von Sekundär- und Primärwaldblöcken darauf hin, dass die Betrachtungsebene maßgeblich mitbestimmt, inwieweit solche Änderungen mit moderner Methodik fassbar sind.

Die insgesamt unerwartet uneinheitlichen Ergebnisse bezüglich der Reaktionsweisen der vier Arten hinsichtlich ihrer Fortbewegungsmuster und Parasitengemeinschaften auf die durch Abholzungen bewirkten Habitatsveränderungen erlauben keine allgemeingültigen Schlussfolgerungen bezüglich der Auswirkungen von Regenwalddegradation auf Kleinsäuger. Vielmehr zeigen sie deutlich, dass multiple Kombinationen aus Umweltfaktoren und artspezifischen Faktoren das Verhalten der Kleinsäugerarten im gestörten Waldsystemen bestimmen. Detaillierte Verhaltens- und Raumnutzungsstudien von möglichst vielen und unterschiedlichen Arten sind notwendig, um die Toleranz von Kleinsäugerarten, insbesondere spezialisierten und seltenen Arten, gegenüber Habitatdegradation näher zu untersuchen und zu quantifizieren. Solche Ergebnisse könnten eine wichtige Grundlage für moderne Naturschutzkonzepte darstellen, die den Schutz von Kleinsäugerarten bei der Bewirtschaftung von tropischen Forstbeständen oder bei dem Erhalt von Primärwäldern mit einbeziehen, um so ihre Funktionen im Ökosystem zu gewährleisten.



Structural and compositional complex canopies in pristine dipterocarp rainforests.

Left: View from an emergent tree in Kinabalu NP. Crowns from small trees reach heights of 15-25 meters, large trees up to 60 m. Top: Lower canopy in Danum Valley.

Secondary forests with tree heights reduced to 25-30 m. Disrupted canopies and pronounced gaps led to differences in plant composition and growth of the understorey, in which fast-growing plants, such as climbing bamboo (*Dinochloa spp.*), sago palms (*Metroxylon spp.*), or rattan (*Calamus spp.*) dominated.

Right: Secondary forest at Kg. Monggis.

Below: Forest at Kg. Tumbalang.



Rainforest logging affects species richness more than dynamics in a small mammal assemblage

1.1 ABSTRACT

The effects of logging and habitat degradation on diversity and communities of small mammals in Asian rainforests are largely unknown. We surveyed speciose assemblages of non-volant small mammals in three primary and three secondary forests on Borneo (Sabah, Malaysia) for two years. We trapped a total of 1,218 individuals representing 28 species. Eleven common species accounted for 95 % of all captures. Species richness and diversity were significantly higher in primary forest (27 species) than in secondary forest (17 species). This was mainly attributable to the smaller number of rarely recorded species in secondary forest (five compared with 16 in primary forest in a total of > 10 captures). However, the common species were present in primary and secondary forests and revealed similar patterns of dominance, evenness, and fluctuations in abundance at both sites. Composition of non-volant small mammal assemblages did not differ greatly between forest types. Assemblages of Muridae and Tupaiidae showed similar population fluctuations in space and time, indicating that the ecology of these taxa may be partially driven by the same environmental factors. The arboreal rat *Niviventer cremoriventer* and the terrestrial tree shrew *Tupaia tana* increased in abundance in secondary forest and might therefore benefit from forest degradation. Although species were patchily distributed within sites, analyses at local and regional scales revealed similar patterns in diversity and assemblage variability, suggesting that effects of forest modification are not scale-dependent. Our results emphasize the importance and conservational value of degraded forest stands that are able to hold a large proportion of small mammals found in undisturbed rainforests. However, rare and more specialized species are vulnerable to forest degradation, with the loss or decrease in abundance of certain groups, such as arboreal small mammals and Viverridae indicating a depauperate habitat.

1.2 INTRODUCTION

Species diversity and the structure of local assemblages of rainforest-dwelling animals are affected by many factors, including habitat complexity, patch heterogeneity and differences in the resulting spatio-temporal resource availability. Tropical rainforests, in which tree diversity provides essential resources, in particular food and structures for almost all other species, consist of dynamic patches that are frequently perturbed by local disturbances, such as tree falls, that briefly interrupt and change the undisturbed forest matrix (Denslow 1995; Charles-Dominique *et al.* 1998; Condit *et al.* 2000; Schnitzer & Carson 2001). The impact of naturally occurring low to intermediate disturbance levels is not necessarily negative but can also enhance diversity through an increase in heterogeneity and patchiness of the environment (e.g. intermediate disturbance hypothesis: Connell 1978; Molino & Sabatier 2001). However, the large scale and high intensity disturbances that are prominent in many commercially logged forests often have overall negative effects on species assemblages, even though logging may resemble naturally occurring large tree-fall gaps if reduced-impact logging is applied (see Sist *et al.* 2003).

Given the ever increasing anthropogenic pressure on natural environments, and, in particular, in view of the continuous degradation of rainforest areas, ecologists and conservationists face a growing challenge to improve our understanding of the effects of human land-use on species, assemblages, and ecosystem functioning. Borneo contributes considerably to the large biodiversity of the southeast Asian region (Myers *et al.* 2000), although many functional groups of flora and fauna have rarely been subjected to detailed studies (Sodhi & Liow 2000). Deforestation in this area progresses more rapidly than in any other rainforest biome worldwide (Curran *et al.* 2004; Sodhi *et al.* 2004). Most forests in Borneo will probably be logged over in foreseeable future, leaving the largest proportion of land area either deforested or covered with degraded forest of little economical and ecological value. The recovery and succession of the remaining forest stands depends on availability of seed and plant sources as well as on presence of herbivores and their predators (Howlett & Davidson 2003; Brearley *et al.* 2004). Loss or changed abundances of some species or functional groups should further have a significant impact on the interactions of remaining species that may face differences in the availability of interacting agents with regard to resources, predators, or competitors.

Small mammals might have a central role in logging-induced rainforest changes in terms of species compositions and successional processes, as some small mammals are important consumers of seeds and seedlings (Struhsaker 1997; Asquith *et al.* 1997; Blate 1998; Curran & Webb 2000; Lambert *et al.* 2005). Increases in abundance of some small mammal species

may therefore increase seed predation and suppress forest regeneration (Struhsaker 1997). Moreover, their impact upon plant regeneration may be related to their consumption of plant material and/or of herbivorous arthropods. In particular, as small mammals exploit tropical rainforests in diverse communities throughout the three-dimensional space (Bourliere 1987), the many different plant structures, including distally growing reproductive units and their associated herbivorous fauna that are central in plant dispersion and forest succession, might be affected at an early developmental stages. The effects of forest fragmentation on small non-volant mammal communities (e.g. Laurance 1994; Lynam & Billick 1999; Goodman & Rakotondravony 2000; Harrington *et al.* 2001) and their surrounding matrices (Gascon *et al.* 1999; Pardini 2004) are increasingly being investigated, whereas few studies have addressed the effects of logging on small non-volant mammal communities in Asian tropical forests (e.g. Wu *et al.* 1996; Zubaid & Ariffin 1997; Laidlaw 2000; Yasuda *et al.* 2003; Bernard 2004) or elsewhere in the tropics (e.g. Laurance & Laurance 1996; Struhsaker 1997; Malcolm & Ray 2000; Ochoa 2000; Lambert *et al.* 2005). Our knowledge of the impact of habitat degradation on small mammal communities remains poor, particularly for dipterocarp rainforests. Most studies included only two sites, viz., disturbed versus undisturbed, although it is becoming increasingly evident that the effects of forest degradation on species diversity and dynamics are strongly scale-dependent (Condit *et al.* 2002; Hill & Hamer 2004). Within primary dipterocarp rainforests, a large portion of small mammals consists of generalists (e.g. some abundant murids and tupaiids) overlapping widely in dietary composition and microhabitat use (Langham 1983; Emmons 2000; Wells *et al.* 2004a). This large overlap and flexibility in habitat use may blur scale-effects within a heterogeneous forest matrix, although patchiness in resource and tree-species distribution may influence population performances (*sensu* Adler 2000). The population demography of small mammals is also expected to differ along habitat gradients depending upon the degrees of specialization and colonization ability of the species (e.g. Seamon & Adler 1996) or their specific preferences for perturbations, such as tree fall gaps (Beck *et al.* 2004).

The floral composition of logged forests differs from that of primary forests. These differences affect not only overall structure and resource availability, but also the scale of habitat heterogeneity (Cannon *et al.* 1998). On the one hand, logging probably leads to simultaneous changes in species composition and a strong increase of species that are tolerant to logging-induced habitat changes (Cottingham *et al.* 2001). Conversely, species composition might change, but the compensatory changes in species populations might maintain the variability of community properties, such as overall abundance, relatively

constant (Ernest & Brown 2001). Whether the effects of habitat alterations are largely compensated for or whether they are prominently influenced by habitat conditions depends upon the extent of environmental perturbation and the tolerance of key species (Brown *et al.* 2001). Therefore, not only an understanding of the species that are able to persist in logged forests, but also an examination of further assemblage compositions and properties are of interest in order to determine whether small mammal communities are maintained at a certain stabilized level. These data are crucial to unravel whether and which functional groups or taxa respond either distinctively or compensatory to logging.

To improve our appreciation of the changes in species performances and assemblage dynamics in degraded forests, we have asked the following questions. 1) Does the diversity of non-volant small mammals (species richness, dominance, and evenness) differ between primary and logged forests? 2) Does assemblage variability (β -diversity) differ between forest types? 3) Which factors determine changes in assemblage compositions? 4) Do distinct taxonomic groups (Muridae and Tupaiidae) differ in their dynamics and responses to forest degradation?

1.3 METHODS AND MATERIALS

1.3.1 Study area

Borneo is the second largest tropical island after New Guinea. It harbours a diverse flora and fauna with approximately 3,000 species of trees (MacKinnon *et al.* 1996) and around 130 non-volant mammal species (Payne *et al.* 1998) comprising both Sundaic elements and a high degree of endemism. The moist tropical climate is characterized by two promoted wet seasons in May-June and October-January (Walsh & Newberry 1999). Droughts induced by El-Nino events affect fruit production as they trigger the synchronous fruiting of dipterocarp trees that serve as important key resources for many vertebrates (Curran & Webb 2000). Despite the extensive and ongoing clearing of forests, remaining forest areas are estimated to cover 48 % of the land surface and comprise forest patches of relatively large sizes (Sabah Forest Department, pers. comm.). Nevertheless, large proportions of the forest are degraded and altered to some extent.

We selected a total of six study sites; three in primary lowland rainforest and three in secondary lowland forest, all situated in northern Borneo (Sabah, Malaysia) at altitudes between 200-900 m (**Fig. 1.1**). All forest stands comprised $>> 1,000$ hectares and were between 17 and 236 km (mean 130 ± 80) apart (primary forests: Poring, Kinabalu NP at 06°

02.248' N, 116° 42.482' E, 'Por'; Tawau Hills NP at 04°23.974' N, 117°53.436' E, 'Taw'; Danum Valley Conservation Area at 04° 57.800' N, 117° 48.173' E, 'Dan'; secondary forests: Kg. Monggis at 06°13.198' N, 116°45.802' E, 'Mong'; Kg. Tumbalang at 06° 08.427' N, 116° 53.912' E, 'Tumb'; Luasong Field Centre at 4° 36.432' N, 117° 23.391' E, 'Luas').

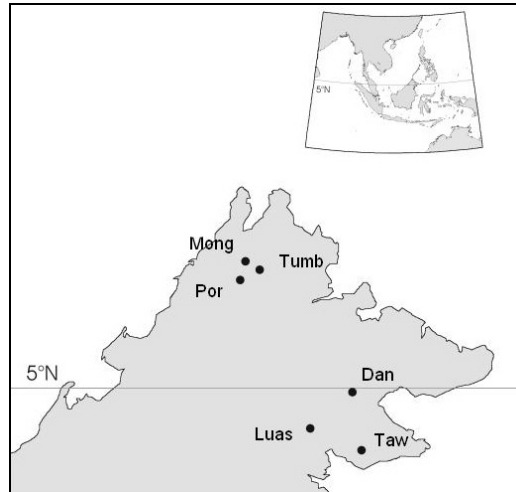


Fig. 1.1. Map of Borneo with the six study sites. Primary forests: Kinabalu NP 'Por'; Tawau Hills NP 'Taw'; Danum Valley Conservation Area 'Dan'; secondary forests: Kg. Monggis 'Mong'; Kg. Tumbalang 'Tumb'; Luasong Field Centre 'Luas'.

Whereas the primary forest stands were characterized by relatively undisturbed vegetation with emergent trees rising up to 60 m, canopy heights at the secondary forest sites, which had been selectively logged ca. 15 – 25 year previous to our study, reached only ca. 25- 30 m, with the few remaining larger trees of no commercial value (e.g. *Ficus spp.*). Details of the logging histories at the various sites were not available, but all secondary sites were of a similar overall structure, and 50% of the original stands appeared to have been damaged, as is usual for conventional logging practice. In comparison with primary forest, disrupted canopies and pronounced gaps in secondary forest led to differences in plant composition and growth of the understorey, in which fast-growing plants, such as climbing bamboo (*Dinochloa spp.*), sago palms (*Metroxylon spp.*), or rattan (*Calamus spp.*) dominated. The hunting of many vertebrates is common in nearly all forest areas, including small non-volant mammals, which are particularly sought in secondary forest sites (pers. obs.).

1.3.2 Animal capture and handling

Animals were captured with locally made, wire-mesh live traps equipped with a plastic roof for rain protection (280 mm × 140 mm × 140 mm) between September 2002 and November 2004. We conducted 18 trapping sessions and alternated between the six study sites (three times at each) with an average interval of 103 ± 50 days between consecutive trapping sessions at the same forest site. Trapping was carried out with a similar seasonal distribution throughout the year for both forest types. At each forest site, we established a randomly located and permanently marked transect of 40 traps set 20 m apart in two parallel lines on the forest floor. Additionally, 30-58 traps were arbitrarily placed at an additional set of two locations that were about 0.5-1.1 km apart from transects except in Poring, where topographic conditions allowed only for distances of 300 m. Additional traps were variously set to enhance data on species diversity. The traps were baited with banana and checked each morning for 16 consecutive days at each trapping session.

The averaged trapping effort was $2,148 \pm 408$ trap-nights per session. Captured animals were anesthetized, marked with a pit tag (AEG, ISO compliant transponders, ARE 162), measured, and then released at the point of capture. Although some rats in arbitrarily sampled sites were only marked by ear punching, they could be reliably identified as recaptures during the entire study period. Species identification was based on Payne *et al.* (1998) and by comparison with specimens from the Sabah Parks Museum (Kundasang, Sabah, Malaysia). Specimen of accidentally killed animals or individuals collected during the last trapping sessions were deposited either at the Sabah Parks Museum or at the Senckenberg Museum, Frankfurt, Germany.

1.3.3 Data analysis

We examined species richness in primary and secondary forests by using sample-based rarefaction curves based on total trapping effort throughout the study time. This approach incorporated spatial heterogeneity, which is inherent to almost all samples (Colwell *et al.* 2004). We then estimated the expected number of species for primary and secondary forest with Chao2 and Jack1 species richness estimators (Colwell *et al.* 2004).

We established data matrices including the number of individuals for each species trapped in transects during the 16-day periods (483 individuals in 18 transects, ‘trans’) and for the first 54 individuals trapped in a trapping session pooled from captures in transects and additional locations (‘sess’). Two trapping sessions were excluded from analysis because of small sample sizes, leaving 864 individuals in 16 sessions for analysis. We distinguished further

between species assemblages of all species, and separately with respect to murids and tupaiids. All analyses were performed at both levels of the ensembles to include the effects of local abundances and point estimates (trans), separately from the relative abundances of species on a more regional scale (sess) independent of local heterogeneity. As some immature spiny rats (*Maxomys rajah* and *M. surifer*) were not distinguishable in the field, we added the unidentified individuals proportionally to the number of identified individuals of both species for all analyses (45 out of a total of 171 individuals, see **Table 1.1**).

We used the Coefficient of Variation ($CV = S.E. / \text{average number of individuals}$) to describe variations in species abundance within sites and the non-parametric Shannon-Wiener index H' to analyze species richness and heterogeneity (Magurran 2004). Bray-Curtis (quantitative Sørensen) similarity matrices were used for comparisons across species assemblages. Based on these matrices, we conducted a two-dimensional non-linear ordination with multidimensional scaling (NMDS), which is a particular robust ordination technique (Clarke 1993). Further, we also ordinated distance matrices of temporal (chronological time differences in days), seasonal (shortest time differences between months of respective sessions), and geographic (kilometres between sites) distances between all 18 trapping sessions into two-dimensional NMDS coordinates and correlated them with NMDS scores from species assemblages. We defined the species specific persistence rate PR of individuals in consecutive sessions as $PR = re * \Delta t / (N_t * N_{t-1})$ where re is the number of recaptured individuals, Δt is the time lag [days] between sessions, N_t is the number of individuals in session, and N_{t-1} is the number of individuals in previous session. Diversity estimates were calculated with the software EstimateS (Version 7.5, R.K. Colwell, <http://purl.oclc.org/estimates>), whereas statistical analyses were performed with Statistica 6.0 (Statsoft 2001). Means are given as ± 1 S.D.

1.4 RESULTS

1.4.1 α -Diversity in different forest types

During the entire study, we trapped a total of 1,218 individuals (3,809 times trapped) from 28 species, representing 17 genera from 8 families with a sampling effort of 40,552 trap nights (**Table 1.1**).

Table 1.1. Number of individuals for all species trapped in the various study areas. The total trap effort for each area is given in parenthesis. Additional trapping efforts in Por and Taw during the period of fieldwork that was not part of the analyses are included to provide a more complete species record.

Species	Total number of ind.	Primary forest (PF)			Secondary forest (SF)		
		Dan (7092)	Por (7545)	Taw (8115)	Luas (6469)	Mong (6040)	Tumb (5291)
Muridae							
<i>Chiropodomys major</i>	1	1	-	-	-	-	-
<i>Lenothrix canus</i>	2	-	2	-	-	-	-
<i>Leopoldamys sabanus</i>	175	9	76	18	12	39	21
<i>Maxomys baeodon</i>	5	1	-	-	1	1	2
<i>Maxomys ochraceiventer</i>	2	-	2	-	-	-	-
<i>Maxomys rajah</i>	76	25	1	3	37	9	1
<i>Maxomys surifer</i>	50	7	4	10	14	9	6
<i>Maxomys cf. surifer/rajah</i>	45	25	4	4	3	8	1
<i>Maxomys whiteheadi</i>	73	12	10	26	18	3	4
<i>Niviventer cremoriventer</i>	265	28	26	9	19	55	128
<i>Rattus rattus</i>	4	2	-	2	-	-	-
<i>Sundamys muelleri</i>	41	3	1	1	-	-	36
Sciuridae							
<i>Lariscus hosei</i>	1	-	-	1	-	-	-
<i>Callosciurus notatus</i>	11	-	5	-	1	4	1
<i>Callosciurus prevostii</i>	4	-	3	1	-	-	-
<i>Sundasciurus brookei</i>	1	-	1	-	-	-	-
<i>Sundasciurus hippurus</i>	7	1	1	4	-	-	1
<i>Sundasciurus lowii</i>	45	8	2	21	5	5	4
Hystricidae							
<i>Trichys fasciculata</i>	2	-	-	2	-	-	-
Insectivora							
<i>Chimarrogale himalayica</i>	1	-	-	-	-	-	1
<i>Echinosorex gymnurus</i>	4	-	-	2	2	-	-
Tupaïidae							
<i>Ptilocercus lowii</i>	2	-	1	-	-	-	1
<i>Tupaia gracilis</i>	24	1	9	4	4	2	4
<i>Tupaia longipes</i>	117	28	10	42	23	4	10
<i>Tupaia minor</i>	76	1	25	2	-	4	44
<i>Tupaia tana</i>	173	22	15	12	15	54	55
Viverridae							
<i>Arctogalidia trivirgata</i>	2	-	1	1	-	-	-
<i>Paradoxurus hermaphroditus</i>	6	4	-	2	-	-	-
<i>Viverra zangalunga</i>	3	3	-	-	-	-	-
Total	1218	181	199	167	154	197	320
Number of species	28	17	19	19	12	12	16

In the primary forests, more species but fewer individuals (27 species, 547 individuals) were recorded than in the secondary forests (17 species, 671 individuals). The only species that was not recorded in primary forests was the shrew *Chimarrogale himalayica*, which was captured only once in secondary forest. It was probably not attracted to our bait, as it is an insectivore. Accumulation curves indicated that the primary forests contained a more heterogeneous small non-volant mammal assemblage with a steeper accumulation curve than for secondary forests, for which sampling was more asymptotic (**Fig. 1.2**).

Estimates of predicted species richness were larger for primary forests with 29 ± 3 (Chao2) to 32 ± 2 (Jack1) estimated species than for secondary forests with 22 ± 6 (Chao2) to 21 ± 2 (Jack1) estimated species. These estimates confirmed that species richness was significantly lower in SF, although the number of trapped species was below the confidence intervals of predicted estimates for both forest types. Estimates of species richness for data sets from the transects (Chao2: 17 ± 3 for PF, 14 ± 1 for SF; Jack1: 19 ± 1 for PF, 16 ± 1 for SF) or standardized sessions (Chao2: 27 ± 4 for PF, 14 ± 0.2 for SF; Jack1: 28 ± 3 for PF, 15 ± 1 for SF) were in part lower than the total number of documented species, which was most probably the consequence of rare and therefore slowly accumulating species that were under-represented in single trapping sessions.

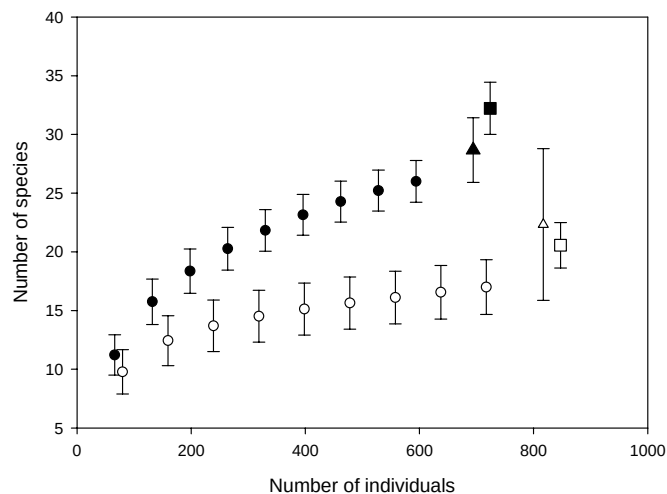


Fig. 1.2. Rarefied species accumulation curves representing the average number of species for a given number of captured individuals for the entire regional trapping effort (sessions) in primary forest (●) and secondary forest (○). Triangles and squares refer to the estimated number of species based on Chao2 and Jack1 estimators, respectively. Bars are 95 % confidence intervals.

We considered eleven species as being common, as they were represented in > 20 captures in total. Those species accounted for 95 % of all captures. Except for *Sundamys muelleri*, they were recorded at all forest sites. Murids were most abundant in both forest types and accounted for 57 % and 63 % of all captures in primary and secondary forests, respectively. Tupaiids were recorded with fewer capture rates (31 % and 33 % of all captures) in primary and secondary forest.

Shannon Wiener's diversity estimates showed no clear differences between sites (Kruskal-Wallis ANOVA_{trans} $H_{5,18} = 2.42$, $p = 0.78$; K.-W. ANOVA_{sess} $H_{5,16} = 10.9$, $p = 0.053$), but overall diversity between both forest types was significantly lower in secondary forest (trans: $H'_{PF} = 2.35 \pm 0.02$, $H'_{SF} = 2.08 \pm 0.05$; sess: $H'_{PF} = 2.43 \pm 0.03$, $H'_{SF} = 2.12 \pm 0.04$).

1.4.2 Dominance and abundance of common species

The most abundantly trapped species recorded in trapping sessions were *N. cremoriventer* ($n = 5$), *M. rajah* ($n = 4$), *L. sabanus* ($n = 3$), *T. longipes* ($n = 3$), *T. tana* ($n = 2$), and *M. whiteheadi* ($n = 1$). The three most abundantly trapped species varied within and between study sites. Whereas they were mostly the same within a study site (Sørensen index $S_{\text{mean}}(\text{site}) = 0.70 \pm 0.19$), the abundant species differed more often between sites of the same forest type ($S_{\text{mean}}(\text{PF}) = 0.39 \pm 0.26$, $S_{\text{mean}}(\text{SF}) = 0.50 \pm 0.29$) with no obvious differences in dominance patterns between PF and SF ($S_{\text{mean}}(\text{PF} \times \text{SF}) = 0.42 \pm 0.27$).

Fluctuations in abundance of the 11 most common species, as determined by the CV, from each site did not differ across sites (Kruskal-Wallis ANOVA_{trans}, $H_{5,53} = 6.39$, $p = 0.26$; K.-W. ANOVA_{sess}, $H_{5,66} = 9.39$, $p = 0.09$). Mean CVs ranged from 0.37 at Taw to 0.66 at Dan for transect data and from 0.23 at Luas to 0.62 at Tumb for sessions with no recognizable difference in abundance fluctuations among species (K.-W. ANOVA_{trans}, $H_{10,53} = 11.65$, $p = 0.31$; K.-W. ANOVA_{sess}, $H_{10,60} = 11.44$, $p = 0.32$). Overall, mean abundance fluctuations pooled for the different forest types did not differ between primary and secondary forests (M.-W.-U, $U = 391.5$, $p = 0.39$).

Likewise, the relative abundance of the most dominant species did not differ between sessions in primary and secondary forests (M.-W.-U, $U = 36$, $p = 0.79$), and overall abundance distributions as indicated by rank abundance curves were not distinct between primary and secondary forests (all Kolmogorov-Smirnov 2-sample tests ($n = 15$) $p > 0.10$) (**Fig. 1.3**). However, mean capture frequencies were significantly larger for *N. cremoriventer* and *T. tana* in secondary than in primary forest (both M.-W.-U, $U > 15$, $p < 0.05$).

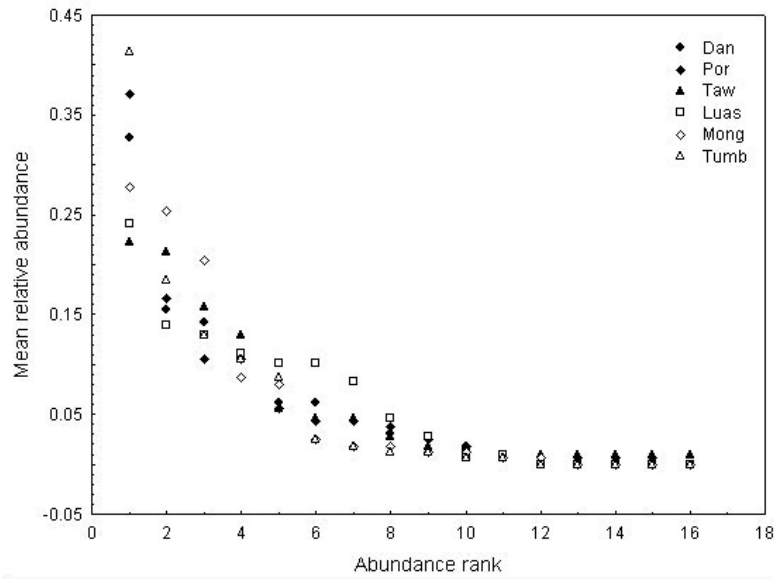


Fig. 1.3. Mean relative abundances of species pooled over trapping sessions at various study sites. No significant differences in the shape of the rank abundance curves were detectable (all Kolmogorov-Smirnov 2-sample tests $p > 0.10$). Note that the number of species is lower than that recorded in some sessions because of data standardization.

1.4.3 Spatio-temporal variation in assemblage structure

NMDS ordinations of species assemblages and seasonal/ temporal similarities between trapping sessions extracted two-dimensional solutions with all the raw stress factors $\phi \leq 0.15$, indicating that original relationships in matrices were sufficiently represented by resulting NMDS axes (Clarke 1993). Changes in assemblage structure at the local level based on transect data (trans, **Fig. 1.4**) were significantly correlated to changes at the regional level based on data from entire sessions by ordination scores (Axes1: Spearman $R_{n=16} = 0.90$, $p < 0.00002$; Axes2: $R_{n=16} = 0.69$, $p < 0.004$).

Whereas the number of tupauid species was correlated with the composition of assemblages at the local level (trans: Spearman $R_{n=18} = -0.60$, $p < 0.009$), the number of murid species was correlated with species composition at the regional level (sess: Spearman $R_{n=18} = 0.68$, $p < 0.004$) (**Fig. 1.5a**). For both censuses (local and regional), changes in assemblage composition of murids and tupauids were significantly correlated on the first axes (trans: $R_{n=16} = -0.54$, $p < 0.03$; sess: $R_{n=16} = -0.68$, $p < 0.004$), suggesting that part of this pattern is driven by similar environmental fluctuations (**Fig. 1.5b**). We traced these relationships down to the species level and found that murid assemblages described by NMDS scores were correlated with the relative abundances of *T. minor* and *T. longipes* (sess: both Spearman $R_{n=16} > \pm 0.75$, $p <$

0.0006). Tupaiid scores were correlated to the relative abundances of *N. cremoriventer*, *M. rajah*, and *M. whiteheadi* (sess: all $R_{n=16} > \pm 0.50$, $p < 0.05$). Species assemblages were also correlated to respective H' diversity estimates, but not to any respective number of captured individuals (see Fig. 1.5a,b).

An impact of geographic distance between sites on ordination scores was detectable for entire species assemblages and for murid and tupaiid assemblages at the local level (trans: all Spearman $R_{n=6} > \pm 0.82$, $p < 0.05$), and for tupaids at the regional level (sess: $R_{n=6} = 0.83$, $p < 0.05$).

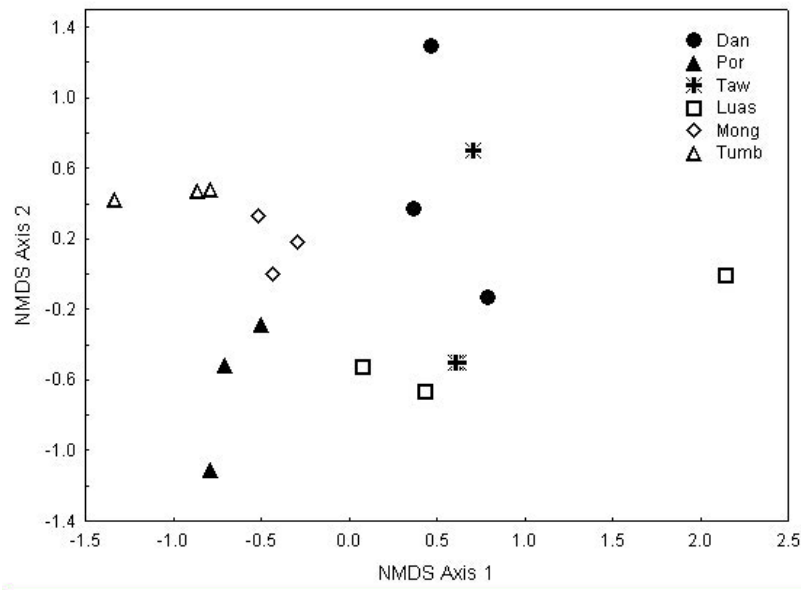


Fig. 1.4. Multidimensional scaling plot of small non-volant mammal assemblages based on local censuses (trans) during the 18 trapping sessions.

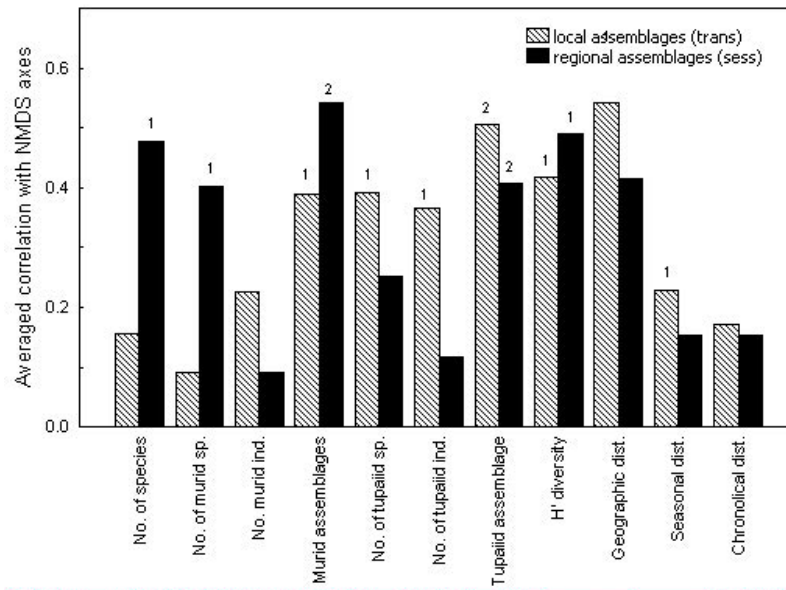


Fig. 1.5a. The impact of selected variables on changes in community compositions of local (trans) and regional (sess) species assemblages. Bars represent the mean of R-values from Spearman correlations of both axes (note: total variability is represented by four comparisons for the ordinated variables of assemblages and distances, and by two comparisons for H' diversity and for species and individual numbers). Numbers of significant correlations ($p < 0.05$) are given above the respective bars.

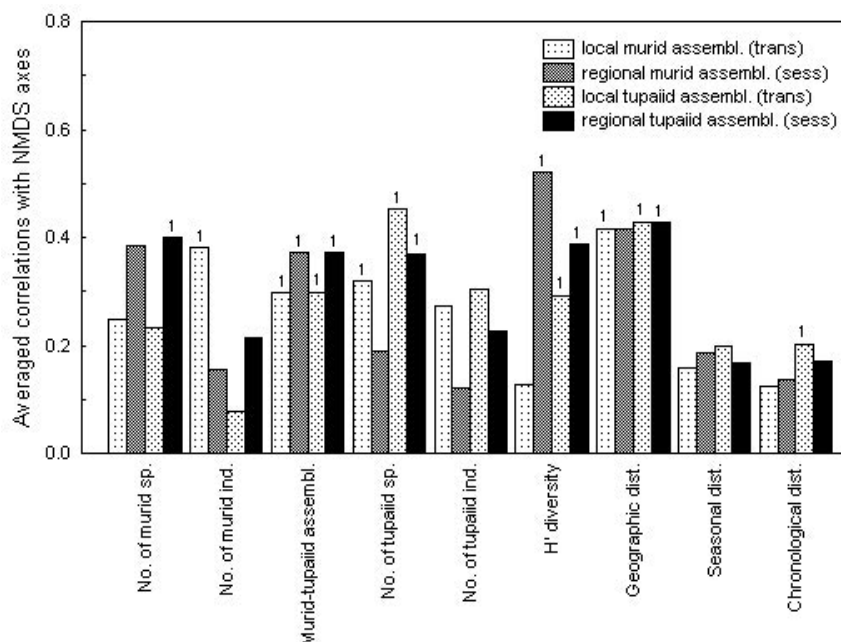


Fig. 1.5b. The impact of selected variables on local and regional changes in murid and tupaiid community compositions. Bars represent the summed R-values from Spearman correlations of both axes (see Fig. 1.5a).

Temporal time differences between sessions were correlated with fluctuations in tupaiid assemblages at the local level (trans: Spearman $R_{n=18} = 0.55$, $p < 0.02$), whereas seasonal time differences (first ordination axis) were correlated with the second ordination axes of the complete assemblages at the local level (trans: Spearman $R_{n=18} = -0.48$, $p < 0.05$). Capture success was lowest during fruiting seasons in September and October (**Fig. 1.6**), although the impact of season on community composition was not statistically significant. Composition of species assemblages was most similar within sites and less similar across sites (site as fixed factor: K.-W. ANOVA Axes 1, trans: $H_{5,18} = 14.45$, $p < 0.02$; sess: $H_{5,16} = 14.01$, $p < 0.02$). Scores of assemblages in primary and secondary forest were indistinguishable from each other at the local level (trans: both M.-W.-U, $U > 25$, $p > 0.17$). However, regional NMDS scores of assemblage composition on the regional level differed between primary and secondary forest on the first ordination axis (sess: M.-W.-U, $U = 11$, $p < 0.03$).

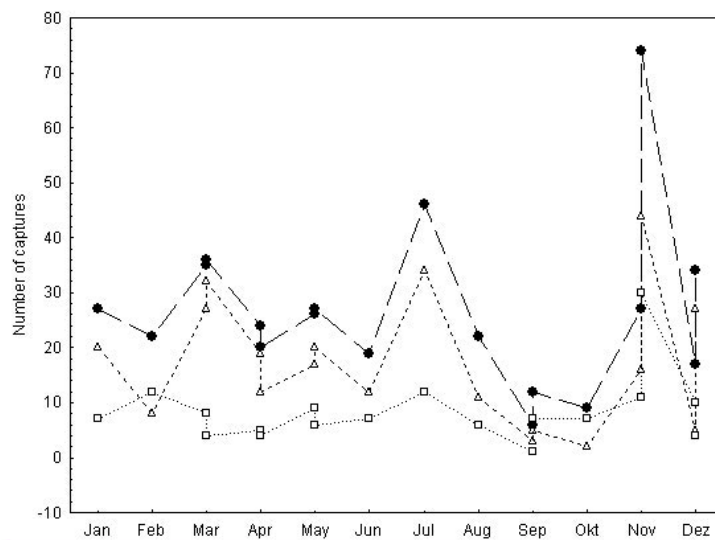


Fig. 1.6. Number of captures in transects throughout the year. The total number of captured individuals (●), murids (Δ), and tupaiids (□) are given. Although the trap success for murids and tupaiids was not correlated (Spearman $R_{(n=18)} = 0.16$, $p = 0.54$) and the verification of general seasonal patterns was weak, the trapping success for both taxa was lowest during fruiting seasons in Sep./Oct. Note: some months contain more than one sample.

Further analyses of determinants for differences in the composition of primary versus secondary forest assemblages involving linear regression analysis of either NMDS-axes relationships (ax1 – ax2) or time lags from similarity indices were statistically not possible. This could have been a consequence of random fluctuations or small sample size.

1.4.4 Distribution of species

The spatial distribution of species was heterogeneous among localities (transects and additional locations) within a study site. A comparison of observed and expected distributions of common species based on the total number of captures at different locations revealed significant deviations from a random distribution among locations within any site in 20 out of 146 cases (all χ^2 tests $\chi^2 > 6.1$, $p < 0.05$). Patterns of spatial heterogeneity regarding species distribution were similar for primary and secondary forest and were most pronounced for *L. sabanus*, *S. lowii*, and *T. gracilis*.

1.4.5 Persistence of individuals

We recaptured 15 % (N=120 individuals) out of 784 marked individuals. Persistence rates of individuals in consecutive trapping sessions differed between forest sites (K.-W. ANOVA $H_{5,110} = 18.15$, $p < 0.003$) as persistence rates were high in Taw but low in Luas, and compared among forest sites, were marginally lower in secondary forest (M.-W.-U, $U = 1203$, $p = 0.07$). The mean persistence rate was largest for *M. surifer*, *M. rajah*, and *T. gracilis*. However, the means differed only slightly among species because of the large variability of persistence rates among sites (K.-W. ANOVA $H_{5,110} = 18.15$, $p = 0.08$) (**Table 1.2**). The longest persistence was recorded for a *T. minor* individual with 636 days, which was marked in a previous study in 2002 (Wells *et al.* 2004a).

Table 1.2. Maximum recorded persistence times for common species.

Species	Max. persistence [days]	Site of record	Total no. of recaptured individuals	Mean persistence rate PR
<i>L. sabanus</i>	534	PF, Taw	14	3.8 ± 5.8
<i>N. cremoriventer</i>	494	SF, Tumb	20	0.5 ± 0.9
<i>M. rajah</i>	573	PF, Dan	23	20.8 ± 41.0
<i>M. surifer</i>	537	PF, Taw	5	20.1 ± 37.8
<i>M. whiteheadi</i>	273	PF, Dan	5	7.4 ± 14.6
<i>S. muelleri</i>	250	SF Tumb	1	0.2 ± 0.7
<i>S. lowii</i>	262	PF, Taw	3	0.6 ± 1.8
<i>T. gracilis</i>	287	PF, Taw	4	19.3 ± 33.1
<i>T. minor</i>	636	PF, Por	6	0.4 ± 1.0
<i>T. longipes</i>	590	PF, Taw	9	2.2 ± 2.8
<i>T. tana</i>	547	PF, Taw	19	6.9 ± 13.7

1.5 DISCUSSION

The great diversity in structure and consumable resources for in tropical forests provided by the variety of floral components has been considered as essential in maintaining diverse small mammal communities (August 1983). In spatially and temporally variable rainforest habitats, the occurrence and assemblage patterns for small mammals are also determined by the degree of specialization and flexibility in species demography (Adler 2000). Such flexibility of species should not only promote persistence and abundance in a heterogeneous forest matrix but also determine tolerance toward logging and habitat disturbance. In our study, rainforest logging resulted in a significant loss of rare small non-volant mammals species in secondary forest, whereas the ubiquitous presence of common species in all forest sites suggests that the assemblage dynamics therein are basically determined by the same species. These abundance fluctuations and assemblage variability seem to be little affected by logging among multiple comparisons of replicates within and between sites, posing the question as to what extent the observed variation is an inherent feature of the local species assemblages and can be traced to certain dominant species. However, in view of the poorly understood life history traits of most species, the multilateral interactions of small mammals with their biotic and abiotic environment, and the methodological limits of trapping data approaches (see Voss & Emmons 1996) make firm conclusions difficult. Despite such shortcomings, the lack of alternatives so far warrants to our opinion studies like this as they reveal some interesting patterns that are well-needed to better understand the effects of rainforest disturbance on small mammals and other vertebrates.

The pronounced decline of species richness and diversity in degraded forests was mainly attributable to the decrease of rare species, whereas common species of omnivorous murids or tupaiids were recorded almost equally well at all forest sites. The observed species decline was consistent with other studies on small non-volant mammals in Australia (Laurance & Laurance 1996), Malaysia (Zubaid & Ariffin 1997; Yasuda *et al.* 2003) and Venezuela (Ochoa 2000). However, despite of such common pattern, there is little evidence for common traits among species that are rare and declining in secondary forests.

Differences in floral composition and structure of the forest resulting from degradation apparently impact habitats of small, non-volant mammals and resource availability in the various forest types. If logged sites mainly lack species with a higher dietary specialization, habitat transformation should strongly affect the occurrence of the most specialized species or species that are linked by certain requirements or characters. Species that were affected by logging fitted several arrangements in groups, but there was no evidence for a single trait

explaining the lack of certain species in logged forests. Four of the rare species that we have recorded only in primary forests are endemic to Borneo (*C. major*, *M. ochraceiventer*, *L. hosei*, *S. brookei*), and their restricted geographic distribution might be associated with a lower habitat tolerance. Among taxa, species decline in logged forest is most evident for civets, which are known to be sensitive to habitat degradation (Heydon & Bulloh 1996; Colon 2002). The mainly arboreal rats (*C. major*, *L. canus*) and squirrels (*C. prevostii*, *S. brookei*) are less prevalent in secondary forests, which might be because of reduced canopy space and altered tree composition and texture (see also Saiful *et al.* 2001; Yasuda *et al.* 2003; Wells *et al.* 2004a, b) compared to primary forest. Primarily, an unsolved question remains regarding whether resource availability or structure and habitat space are the main determinants of reduced species richness in secondary forest and whether these proximate parameters are indeed most affective on particular species groups. Some studies suggest that the consequences of habitat disturbance differ with the type, spatial extent, and degree of disturbance. Under favourable circumstances this may also lead to increases in non-volant small mammal abundances in disturbed habitats (e.g. Struhsaker 1997; Malcolm & Ray 2000; Lambert *et al.* 2005). Such increases have been associated with an increase of herbaceous vegetation, a decrease in canopy and sapling density, and more abundant arthropods and fruits (see Struhsaker 1997; Malcolm 1997; Lambert *et al.* 2003). Despite the reduced species richness in secondary forest, we have found an increased abundance for *N. cremoriventer* and *T. tana* in logged forests. *T. tana* has been suggested to prefer dense undergrowth and gap structures (Emmons 2000; Wells *et al.* 2004a). However, whether particular resources or structural features are per se important and whether conclusions from gap versus understorey dynamics are applicable to logged forest conditions remain unclear.

Generally, habitat heterogeneity and the resulting resource availability should be a prime factor influencing the population structure of small mammals along disturbance gradients. If we hypothesize that species declines in degraded forests are attributable to resource specialization, it would be of further interest to consider whether the occurrence and abundance patterns of any species are driven by the presence of particular resources or principle patterns of resource allocation. Tree species, for instance, that play a significant role in overall forest architecture and resources, are not randomly distributed within primary forests, in which aggregation is most prevalent for rare species (Condit *et al.* 2000). Rather than forest structure, such distributional patterns have been shown to influence the demography of a neotropical *Proechimys* rat in terms of resource availability, in particular with regard to figs *Ficus spp.* (Adler 2000). Non-volant small mammals with specialized

feeding habits and a dependence on spatially clumped resources should be most aggregated. Conversely, common species with omnivorous diets should cope well with different resources and exhibit greater tolerance towards spatio-temporal resource variability. If spatial variability in plant and other resources exceeds foraging areas of generalist feeders, ubiquitous species should be able to cope with different resources that might compensate for each other's absence. This flexibility should promote presence and abundance in a heterogeneous forest. Thus, the chance of capture of a species should decrease for more specialized species because of reduced abundance or may occur because an occupied patch with essential resources is not being covered by the sampling area.

Disturbance such as logging might affect these distributional patterns. Logged forests not only comprise a different floral composition and distribution of components (Cannon *et al.* 1998), but also differ in their proportion of animal-dispersed and mammal-pollinated trees (Chazdon *et al.* 2003) and in the arthropod assemblages that may partially serve as food sources for small mammals (Willott *et al.* 2000; Davis *et al.* 2001; Cleary 2003). For instance, reduced availability of particular fruit resources in logged forests has been reported negatively to influence densities of fruit-eating mouse deer *Tragulus spp.* (Heydon & Bulloh 1997). With the same argumentation as for spatially clumped resources within a habitat type (see above), such resource alteration should mostly influence the incidence and density of more specialized small non-volant mammals. For generalists, resources might still be present on an altered scale or compensated by alternative resources.

Such considerations seem to be pertinent to our results, as common species have revealed some aggregation of individuals but are also widely dispersed in different locations and forest sites. Reduced species richness in logged forests appeared to occur mostly as a consequence of reduced densities or the stronger aggregation of rare species, as most of the rare species trapped only in primary forests are known to be also present in logged forests (*L. canus*, *C. prevostii*, *T. fasciculata*, all civets; pers. obs.).

Tolerance toward logging by common species and the pronounced prevalence of rare species in primary forests has also been found for bird species in the same geographic region (Sodhi 2002; Lammertink 2004). However, scaling leads to contrasting results with both decreased and increased diversity recorded in a wider array of studies conducted on different spatial scales with birds and butterflies (Hill & Hamer 2004).

The amount of intra-specific aggregation of taxonomically similar species among a set of assemblages should decrease α -diversity and increase β -diversity at the same time (Veech 2005). Therefore, the spatially clumped distribution of species should also be considered for

the interpretation of variability in assemblages both within and among forest types. Surprisingly, overall assemblage variability differ neither between primary and secondary forest nor local and regional level. Furthermore, we have found no differences in abundance fluctuations of common murids and tupaiids within a forest type and no evidence for different impacts of logging on these functional groups, but some relationships in assemblage fluctuations of both taxa. Variability in assemblages at the local level can partially be explained by the number of tupaiid species, whereas murid species are more influential on assemblage fluctuations on the regional scale (see Fig. 1.5a).

Given the observation that different taxa of plants or invertebrates respond inconsistently to anthropogenic habitat alteration (Lawton *et al.* 1998; Ricketts *et al.* 2002), the availability of food resources for murids and tupaiids might not necessarily be synchronously altered in disturbed habitats. Although the food spectra of these species are only fractionally known with some assumed overlaps (Langham 1983; Emmons 2000), remarkable differences exist in the morpho-physiological traits related to food processing. Tupaiids have weak jaws in combination with short intestinal transition times and simplified colons (Emmons 1991) that do not allow the processing of the hard dipterocarp and lithocarp fruits that are heavily fed upon by murids during the fruiting season in primary forests (Curran & Webb 2000; K. Wells & R. Bagchi, pers. obs.). However, although these fruits comprise a key resource in primary forests, their impact neither results in detectable differences in murid fluctuations between primary and secondary forest nor in any asynchronous changes in murid and tupaiid assemblages. Nevertheless, some seasonal impact that seems to be related to fruiting can be assumed because of the reduced trapping success during this period; in particular, murids in primary forests show increased reproductive activity during this time (pers. obs.).

Another factor of prevalence for community change in our study was the geographic distance between study sites, which seemed to lessen any logging-induced changes. Geographically distinct areas differ in climate, altitude and edaphic factors that might further influence plant and resource composition on a regional scale (Ashton & Hall 1992; Newberry *et al.* 1996). One primary (Por) and two secondary forest sites (Mong, Tumb) lay near to each other (17 – 24 km) and to Mount Kinabalu, which is of importance, for example, for the topography, soil mineral content, and climate of this region (e.g. Kitayama 1992). As assemblages from different sites seemed to cluster near to each other with decreasing distance, such geographically related factors might in this area be currently of greater importance than logging-induced alterations on abundance fluctuations and assemblage dynamics. Regarding the aspects of a larger geographic scale suggests that a considerable level of variation is

naturally inherent to small mammal communities, although scaling was of little impact from a local to regional scale in this study.

Furthermore, overall assemblage variability did not differ between primary and secondary forests, and no differences in abundance fluctuations or dominance patterns were apparent. The parallelism in assemblage features between forest types suggests that fundamental ecological or abiotic features of the biome, rather than differences between primary and secondary forest, are major driving forces. If forest degradation had revealed a stronger influence on small mammal fluctuations, one would expect more pronounced fluctuations occurring in parallel to relevant successional changes or continuous anthropogenic disturbances.

Although logged forest are generally characterized by considerable changes in composition and physical structure, many kinds of logging damage might in some ways be equivalent to naturally occurring perturbations and alterations to which a large proportion of common non-volant small mammal species are well adapted. Most of the commonly reported species from our study occur over a wide geographic range (Musser & Carleton 1993). The vicariance of common rats such as *L. sabanus*, *M. surifer* or *M. whitheadi* over a larger geographic range throughout their evolutionary history (see Gorog *et al.* 2004) supports the idea of a long-term adaptation and tolerance of these species toward changes in habitat conditions. These species comprise a large proportion of assemblages in both the primary and secondary forests studied here, with similar compositional patterns. They were also dominating the comparative analysis between forest types. To conclude, logging did not consistently cause strong changes in species assemblages. However, as we know little about the multiple interactions of small non-volant mammals with other compounds of the ecosystem, the question remains regarding whether fundamental ecosystem processes in logged forests are altered by reciprocal changes in resource availability, competitors, or carnivorous predators, even if the same small mammal species are present (see Terborgh *et al.* 2001). The role of rare species remains even more elusive, although the reduced species richness in our study clearly suggest that some species are vulnerable to severe population reductions or extinction by logging-induced changes. The inconsistency in logging responses among species and the large variety that is intrinsic to rainforests and that is further generated by various anthropogenic impacts present a challenge for selecting areas and landscape matrices as one of the main concerns for conservation. Hitherto, general statements on logging effects have been possible for neither different species assemblages nor areas. Although logged rainforests might house large proportions of original small non-volant mammal communities, some rare species will remain

undetected and be unprotected if primeval rainforests are not ad infinitum considered as major sources of such species and communities in a naturally stable condition.

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Top left to bottom right:

- *Maxomys whiteheadi*.
- Preparation of cage traps.
- *Tupaia longipes*.
- *Lariscus hosei*.
- *Echinosorex gymnurus*.
- *Maxomys surifer*.

Appendix 1

Small mammals in the rainforest canopy: a neglected group of conservational concern?

(Wells, K., Lakim, M.B., Bernard, H. & Pfeiffer, M. (2004). *ASEAN Review of Biodiversity & Environmental Conservation*, online at <http://www.arbec.com.my/smallmammals/>)

A.1 Abstract

Small mammals of various taxonomic groups and functional types are an important constituent of the rainforest canopy. Little is known about their ecology and distribution patterns, and they are hardly considered in conservational issues. Here we present some ideas and features that might be relevant for considering these group as particularly vulnerable to rainforest disturbance. An example of a highly diverse small mammal assemblage in a canopy is given from Borneo. We conclude by highlighting the importance of three-dimensional modeling of this habitat to understand the biology of arboreal small mammals and also the consequences of habitat changes in the rainforest canopy.

A.2 Introduction

Large mammals in the tropical rainforests of Malaysia hold the attention of the public with their charismatic appearance and unique life histories - and also because of their key role in wildlife conservation. With the need for large undisturbed areas, they are especially susceptible to human induced habitat changes and hunting activity, and nowadays, many species remain only as heavily reduced and threatened populations (Fimbel *et al.* 2000; Laidlaw 2000). These problems are relevant for both species living on the ground such as the well-known species of elephant, tiger or rhino as well as for conspicuous canopy dwellers like apes and monkeys – all species that are frequently brought to the public awareness by the media. However, much less is known about non-volant small mammal species (weights of < 5 kg). Although they occur in complex

communities with exceptional high species richness and considerable impacts on the rainforest ecosystem (Zubaid & Ariffin 1998; Bernard 2004; Wells *et al.* 2004a), they have received little public or conservational attention. The lack of knowledge about these species is a consequence of the difficulties connected with conducting studies in the rainforest environment. Most species are highly cryptic in their appearance and behavior, hardly visible for the human observer who is hindered by the dense and evergreen vegetation. Further, some species are active at night, hiding in burrows or tree holes during the day. Even the capture and systematical study of those species requires a considerable effort with generally low trap success.

A true challenge is faced when posing any question on small mammals in the rainforest canopy well above the ground. The complex canopy of the dipterocarp rainforest rises into the three-dimensional space of up to 60 meters and more with numerous tree crowns of different shapes and heights, and there is extensive variety in structure and plant composition along the vertical axis (e.g. Ashton & Hall 1992). Most of this heterogenous habitat is neither visible from the ground nor accessible without special equipment and effort. No wonder, that the capture and observation of mammals took basically place below heights of 20 meters in most studies conducted so far.

Nevertheless, in both neotropical and paleotropical rainforest sites, small mammal communities are considered to comprise as many or even more species in the canopy than communities on the ground (Harrison 1962; Kays & Allison 2001).

But what do we really know about these canopy dwellers? Only few scientific studies have focused on small mammals occurring in the canopy, and the lack of information is limiting the discussion of this group for wildlife conservation. A considerable number of canopy species are rarely recorded or documented and their life histories or actual distribution patterns along the vertical axis of the canopy are largely unknown. There is even an ongoing debate whether species assemblages occurring on the ground and in the canopy differ and can be separated into distinct communities (Malcolm 1995; Woodman *et al.* 1995; Mauffrey & Catzeflis 2003; Wells *et al.* 2004a).

This is very unfortunate, since we do not preserve what we do not know, although we have to expect a diverse and unique small mammal fauna in the rainforest canopy with an important ecological role and some unrecognized threats to their populations. Therefore, it is important to understand the effects on habitat changes on arboreal mammals and the consequences for the

entire rainforest environment. For management strategies, it would be important to link species demography with the identification of species groups that share habitat requirements and intolerance to particular canopy changes.

The question whether arboreal small mammal species are of conservational concern should be addressed by different approaches: 1) Patterns of species distribution and diversity can be derived and extrapolated from observation and capture data as well as from principle traits of species that can be interpreted as adaptations to certain habitat types of the rainforest canopy. 2) Knowledge of certain components of arboreal small mammal communities in the tropics and facts about sympatric ground species provide insights into ecological principles that can be applied to a broader range of species. 3) Potential threats to arboreal mammals due to habitat loss and modification should be analyzed by considering biotic and abiotic parameters that differ between primary and secondary forests. We then might consider in how far certain species might be either threatened or favored by these habitat changes.

A.3 Borneo: a hotspot of diversity and endemism

The seed for any successful approach in scientific or conservational issues is a proper model. The small mammal community in the rainforest on Borneo comprises an excellent system for many questions, as it is an exceptional species-rich community from various taxa (Wells *et al.* 2004a), consisting of both endemic species (approximately 30 %; Groves 1985) and species with a wide geographic range (Payne *et al.* 1985). The most abundant group comprises rats and mice (Muridae), that can be found on the ground but also in the canopy. In contrast, tree shrews (Scandentia) have basically diversified on the ground, with only two out of five abundant lowland species exploring the canopy space, *Tupaia minor* and *Ptilocercus lowii* (see Sargis 2002; Wells *et al.* 2004a). Squirrels are rarely trapped on the ground, but can be frequently observed in the canopy, where diversification of this group took place. Other taxonomic groups are represented by few species that are rarely recorded, such as the flying lemur, *Cynocephalus variegates*, the western tarsier, *Tarsius bancanus* or the slow loris, *Nycticebus couang* (see Wiens & Zitzmann 2003).

In a strict sense, the term ‘arboreal’ would only apply to those mammals that are primarily active in the canopy. However, such a determination is often not possible because of the mixed activity

patterns on the ground and in the canopy of some species and insufficient knowledge for others (see **Table A.1**).

For instance, the lesser tree shrew, *Tupaia minor*, or some rats like the long-tailed giant rat, *Leopoldamys sabanus*, forage on the ground as well as in the canopy, and most true canopy species descend occasionally to the forest floor to cross gaps or in search of borrows (e.g. the large pencil-tailed tree mouse *Chiropodomys major*; Wells *et al.* 2004b). Therefore, no clear line can be drawn between ground and canopy species. It rather has to be asked, how gradients in species occurrences lead to different small mammal communities within the different strata and whether these patterns can be related to structure or other parameters of the different layers.

Table A.1. Small mammal species live-trapped in the lower canopy between 5 and 25 m heights in the course of our research. Five species were not recorded for secondary forest sites, marked with *. The proportion of arboreal activities (black part of the bar) were roughly estimated from capture data and observations. A total of 126 individuals were captured during > 5.000 arboreal trap nights.

English name	Scientific name	Family	No. of ind. captured	Proportion of arboreality
Large pencil-tailed tree mouse	<i>Chiropodomys major</i> *	Muridae	43	□■■■■■
Dark-tailed tree rat	<i>Niviventer cremoriventer</i>	Muridae	28	□□□■■■
Grey tree rat	<i>Lenothrix canus</i>	Muridae	13	□■■■■■
Long-tailed giant rat	<i>Leopoldamys sabanus</i>	Muridae	6	□□□□■■
Mueller's rat	<i>Sundamys muelleri</i>	Muridae	2	□□□□□■
Plantain squirrel	<i>Callosciurus notatus</i>	Sciuridae	2	□□□■■■
Horse-tailed squirrel	<i>Sundasciurus hippurus</i>	Sciuridae	2	□□□□■■
Brooke's squirrel	<i>Sundasciurus brookei</i> *	Sciuridae	1	□□■■■■
Prevost's squirrel	<i>Callosciurus prevostii</i> *	Sciuridae	1	□□■■■■
Red-cheeked flying squirrel	<i>Hylopetes spadiceus</i> *	Sciuridae	1	■■■■■■
Lesser treeshrew	<i>Tupaia minor</i>	Tupaiaidae	15	□□■■■■
Pentail treeshrew	<i>Ptilocercus lowii</i>	Tupaiaidae	9	□■■■■■
Small-toothed palm civet	<i>Arctogalidia trivirgata</i> *	Viverridae	1	□□□□■■
Slow loris	<i>Nycticebus coucang</i>	Lorisidae	2	□□■■■■

Some species (e.g. the low's squirrel, *Sundasciurus lowii*) are basically found in heights between 1 and 5 m, where they can easily move on logs, dead branches or small trunks. Other squirrels like pygmy squirrels (*Exilisciurus spp.*) or the horse-tailed squirrel, *Sundasciurus hippurus*, can be frequently observed at heights of up to 10 meters, jumping from trunk to trunk. A few squirrel

species occurring in the canopy are separated in their home ranges by tree crown features (Saiful *et al.* 2001). Other arboreal species are hardly trapped in the lower canopy, indicating that these species must be either very rare or more restricted to the upper canopy layers.

Here, it is worthwhile to consider the unique canopy structure of the dipterocarp forest. While tree crowns in the lower canopy between ca. 10 and 25 meters are usually well connected, most of the tall emergent trees (especially of the genera *Shorea* and *Koompassia*) have exposed tree crowns that are well above the closed canopy layer and separated from each other. Interestingly, there is not only the flying lemur, *Cynocephalus variegatus*, but also 12 species of flying squirrels (Petauristinae) recorded for Borneo that have gliding membranes between their limbs – an apparently useful adaptation to cross gaps in the upper canopy. Other special adaptations exhibited by some species include relatively short feed, prolonged tails, prehensile extremities as well as some grasping and jumping ability - features that allow to move on vertical trunks, unstable thin branches or to cross open space.

The effects of environmental changes on arboreal mammals can be expected to be versatile and of various characters. Basically, the canopy dweller in a logged forest faces changes of its habitat that are of structural/ geometrical type or related to the altered resource availability. Both parameters revealed evident relations to small mammal occurrences on the ground (e.g. Adler 2000; Beck *et al.* 2004), but have yet to be evaluated for arboreal species.

A.4 The canopy environment

The canopy environment requires not only adaptations to move around, but also to maintain the physiological balance of the body ('homeostasis'). The canopy dweller must cope with less water resources as well as exposures to wind, rain, sun and higher temperature fluctuations compared to species on the ground. Further, the canopy seems not to support species that rely completely on a carnivorous/insectivorous diet, and all canopy species depend to some extent on primary products such as fruits, leaves, bark or nectar (see Emmons 1995). Though their potential for seed dispersal remains largely unknown, frugivory and the abundant fruit crops in the canopy suggest that arboreal small mammals are important seed dispersers, as recorded for some ground species (e.g. Blate *et al.* 1998; Guariguata *et al.* 2000; Shanahan & Compton 2000, 2001).

As resources in primary forest are generally expected to be scattered or only seasonally available, most species rely on a mixed diet from different resources to fulfill their nutritional requirements.

Of course, all these parameters of the canopy will change when a mammal is moving within the different canopy strata - and even more infinite, these ecological correlates of mammalian biology in the canopy space can be assumed to differ considerably in logged forests. Not only can we find severe changes in structure within the different strata of disturbed forests, but the upper strata are completely lost, typically with an upper limit in tree heights of 30-40 meters. The tree species composition usually differs in secondary forest, favoring the growth of light-tolerant species (e.g. pioneer *Macaranga* trees). Tree crowns differ in their structure due to these taxonomic differences and the lack of upper strata. Branches, that function as pathways for non-gliding mammals grow less horizontal, probably also altering the interconnectivity between trees and gaps in logged forests (pers. obs.). Further, moving around and foraging on terminal branches might be influenced by different bark surfaces or support diameters that influence the grasping ability (see Lemelin 1999; Sargis 2001). The lighter canopy changes the microclimate in all remaining strata, as they are less protected from weather impacts, also increasing the growth of plant species that are basically restricted to gaps in primary forests (rattan, *Calamus spp.*; climbing bamboo, *Dinochloa spp.*; sago palm, *Metroxylon spp.*). In contrast, the higher tree diversity and maturation in an primary forest increases the variability in tree heights and crown structures. Basically, habitat heterogeneity increases towards the upper canopy in a primary forest, whereas complexity is reduced in the canopy but somehow increased in the lower strata in a disturbed forest. Changes in the canopy do not only affect the 'skeletal' parameters like branches and vines, but there is also a decreased and less complex canopy surface in secondary forests (e.g. Birnbaum 2001), the most important area of photosynthesis and primary production. Food resources, especially fruits, and their abundances differ, apart from having a different chemical composition of leaves and other plant material (recognizable by the different shade of primary and secondary foliages).

A.5 A geometric perspective of the canopy

As mentioned before, we do hardly have any knowledge which canopy mammals are either threatened or favored by theses environmental changes. However, one of the major aspect is the reduced canopy space in the vertical dimension. Canopy space is not only extremely converted but also vastly lost whenever a primary forest is disturbed, reducing its volume to half the space or less even if there is no loss of ground area. Currently, most loss of natural habitat and the

consequences for species extinction is discussed by two-dimensional surfaces, based on the scientifically popular species-area-relationships (see Rosenzweig 1997 for a recent review). Various geometric aspects of such two-dimensional areas have been applied to tropical mammal conservation, considering required habitat space ('surface'), edge effects ('circumference'), as well as effects of roads and corridors ('lines'; see Grieser Johns 1997; Laurance & Bierregaard 1997; Cuarón 2000; Laidlaw 2000). But these models are insufficient for the canopy space that apparently requires consideration as a volume. Many aspects in the canopy, considering the structural parameters mentioned above as well as the arboreal mammals' activities connected to these parameters are sensitive to this spatial scale. However, no general ideas have emerged for dealing with scale-dependence in the canopy, whereas such techniques are successfully applied to describe processes within organisms, based on the widely known relationship between metabolic rate and body mass. The allometric exponents in such models are generally determined by the properties of transport compartments that control flow and reactivity of the media (see West *et al.* 2003 for an application ranging from cells to organisms). The movement and foraging success of a small mammal in the canopy might be seen from a similar perspective, and we suggest that such laws might be helpful to describe features of arboreal mammal occurrences and limitations due to canopy disturbance on both a theoretical and empirical basis.

A.6 Conclusion

Though the consequences of habitat changes on small canopy mammals remain largely unknown, their conservation should matter. As a diverse and abundant animal group inhabiting all canopy layers, consuming various plant material and invertebrates, and serving as protein sources for larger animals, they comprise keystone roles for rainforest maintenance and regeneration. In order to eliminate or reduce negative effects of habitat disturbance, it is important to understand the way in which these animals are embedded in the rainforest ecosystem and respond to habitat changes. It should be worthwhile to integrate a three-dimensional view and its underlying dynamics in future research on arboreal mammals. Not only is it crucial to understand on an empirical and theoretical basis how structure and space of the rainforest canopy is altered by human impacts, but also how arboreal mammals and other species respond in their activities and occurrences in this rather complex habitat space.

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Top left to bottom right:

- *Tupaia minor*.
- *Paradoxurus hermaphroditus*.
- *Leopoldamys sabanus*.
- Ascending a tree for trap placement.
- *Lenothrix canus*.
- *Chiropodomys major*.

Movement trajectories and habitat partitioning of small mammals in primary and secondary rainforests on Borneo

2.1 ABSTRACT

Small mammals in tropical rainforests differ in their ability to exploit the habitat above the forest floor. 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 the availability of supportive structures. 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 rainforest of Sabah, Malaysia with a total of 13,525 m path being followed. We also analysed specific changes in their movement patterns in relation to habitat stratification between primary and secondary forests. Animals were trapped in six rainforest areas and equipped with a spool-and-line-device before release. Variables related to climbing activity of the tracked mammals as well as the supportive structures of the vegetation and undergrowth density were measured along their tracks. Movement patterns of the animals differed significantly between all species with most similarities being found for congeneric species that converged strongly in body size and morphology. All species were affected in their movement patterns by the altered forest structure in secondary forests with most differences found in *Leopoldamys sabanus*. The diameter of supportive structures, which was on average smaller in secondary forests, was the only variable that affected all species in a similar way. Overall shifts in microhabitat use showed no common trend among species. Multivariate analysis (factor analysis) revealed contrasting trends for convergent species, in particular *Maxomys rajah* and *M. surifer* and *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.

2.2 INTRODUCTION

Primary rainforests are well known not only for their outstanding biodiversity, but also for their complex structure with multiple layered, above-ground habitats and intricate resource distribution. Within these ecosystems, small mammals form diverse species assemblages with various taxa that successfully exploit the entire space from the ground to the canopy. Consequently, the role of environmental variability in structuring populations and communities has gained much interest among ecologists (August 1983; Bourliere 1989; Eisenberg 1990; Emmons 1995). An understanding of the species-rich assemblages of animal communities in tropical rainforests is still in its early stages, although the ongoing loss and conversion of the remaining primary rainforests leaves little time and space to investigate species in their primeval environment. Particularly in SE Asia, where current land use practices are causing a rapid loss of primary rainforests (Curran *et al.* 2004; Sodhi *et al.* 2004), the composition of local small mammal assemblages and resource partitioning among species that permits co-existence are still poorly understood. Most species are very little studied and/or observations on life history patterns are often anecdotal. However, the study of such species and life history patterns is of fundamental importance not only for understanding how the unique life history patterns have evolved and how they facilitate coexistence in diverse communities, but also for assessment of specific responses by wildlife to habitat changes and the potential of species to cope with altered forest habitats on a long-term basis. Landscape mosaics consisting of primary forest remnants and forest fragments at various degrees of disturbances provide an experimental setting for investigations of communities from local to regional scales. This setting is necessary to shed light on the mechanisms that permit co-existence of sympatric species in a variable environment.

Species segregation in small mammal communities has been largely viewed as trade-offs within communities caused by environmental constraints on the level of individuals, including local habitat characteristics, resource distribution and the presence of predators (Price & Kramer 1984; Kotler & Brown 1988). Efforts to characterise niche utilization of sympatric species in tropical rainforests have been mainly based on relationships between local abundances of small mammals and consecutive habitat features, attributing partitioning mainly to structural habitat features (e.g. Tomblin & Adler 1998; Shanker 2001; Williams *et al.* 2002) or floral diversity and resource availability (e.g. Adler 2000; Kanowski *et al.* 2003; Beck *et al.* 2004). The differential use of forest strata by small mammals and their stratification have been repeatedly reported for both neotropical (Charles-Dominique *et al.* 1981; Janson & Emmons 1991; Malcolm 1991; Cunha & Vieira 2004) and paleotropical

(Rudd & Stevens 1994; Malcolm & Ray 2000; Saiful *et al.* 2001; Wells *et al.* 2004) forest sites, with the differential substrate use by syntopic species being suggested to require a finer scale of segregation than a simple arboreal-terrestrial dichotomy (Charles-Dominique *et al.* 1981).

Approaching any above-ground habitat will have different pay-offs for the various species, as has been mostly discussed in the context of body size limitations. For instance, mammals with larger body size are limited in access to small branches, whereas small-sized bodies associated with higher metabolic rates make it difficult to forage effectively on a more herbivore-dominated diet in the canopy (Eisenberg 1987; Emmons 1995). Apart from body size, morphological characters (e.g. feet shape and proportion, grasping ability) may also support vertical partitioning, driven by trade-offs in effectively moving on flat surfaces versus climbing on small-diameter supports (see Lemelin 1999; Sargis 2001a).

However, most studies are limited to trapping data and frequently comprise only small-scale estimates of habitats along recording sites. The results of these studies might therefore be biased either by insufficient spatial scale or by attracting mammals to baited traps away from their natural path. Both factors prevent the detection of subtle differences in habitat occupancy. Furthermore, trapping studies give a very limited view of limited and finite vertical layers and species assemblages therein embedded that do not represent the continuous gradients in vertical habitat use by small mammals. Despite the widespread concept of a rather fixed microhabitat segregation derived mostly from data on local scales, the importance of data on larger spatial scales has been stressed to explain why species might use a certain type of microhabitat in one location and a different habitat in another one (Bowers & Dooley 1993; Jorgensen 2004; Kneitel & Chase 2004; Rahbek 2005). This aspect is particularly crucial for animal communities in tropical rainforests, where species inhabit a three-dimensional complex, heterogeneous habitat.

It is well known that the distribution of the large numbers of trees, that are fundamental for the occurrence of small mammals through overall resource availability and habitat structure, varies already within single habitats, and further up to larger, geographic scales (e.g. Hubbell 1979; Newberry *et al.* 1992; Potts *et al.* 2002; Palmiotto *et al.* 2004). This variability is most prominent between primary and logged forests (e.g. Uuttera *et al.* 2000; DeWalt *et al.* 2003). Thus, strong specialization seems to be untenable for most tropical small mammal species in an environment of enormous floral diversity, with the majority of resources being represented only in small numbers within the range of a forager. In such an environment, tolerance towards environmental variability should be enhanced by omnivorous feeding habits and

pronounced agility. This pattern is present in most of the common groups of small mammals, including murids, didelphids or tupaiids (e.g. Eisenberg 1990; Emmons 2000).

Several studies have shown that species vary in their responses to forest disturbance and alteration (e.g. Laurance & Laurance 1996; Wu *et al.* 1996; Zubaid & Ariffin 1997; Laidlaw 2000; Malcolm & Ray 2000). For instance, habitat degradation has been found to be a major cause for extinction risks among Australian marsupials (Fisher *et al.* 2003). Not only do differences in floral composition result in an altered resource distribution, but there are also considerable differences in structural components throughout the gradient from the ground to the canopy. Moving efficiently through these structurally altered forest habitats, as is necessary, for example, for resource exploitation, territory establishment or the search for a mate, will depend on the potential of a species to adapt to a variable environment.

Structural habitat changes in secondary forests occur on both the horizontal axis and the vertical axis. Thus, the effects of these changes on small mammals may differ depending upon the magnitude of the physical or energetic constraints faced by the species within or between foraging strata and other species-specific traits. Hence, an analysis of movement trajectories of selected small mammals in various habitats should reveal the separation of species by their substrate use and should permit investigating the proximate mechanisms leading to such patterns. This might ultimately contribute to a better understanding of interspecific variation in adaptability and explain part of the reasons of the decline in small mammals in altered rainforest habitats.

The present study examines the movement trajectories of eight syntopic small mammals in primary and secondary rainforests in Borneo by using the spool-and-line technique. This technique has proven a useful tool for discriminating Brazilian syntopic small mammals in their vertical segregation and their use of supportive structures (Miles *et al.* 1981; Cunha & Vieira 2002). Our main objective was detection of interspecific differences in substrate use and further testing whether movement trajectories differ in primary and secondary forests and whether all species are affected in a similar way.

2.3 METHODS AND MATERIALS

2.3.1 Study area

The lowland rainforest in Sabah (Malaysia) in northern Borneo has been widely logged for timber harvesting and because of land conversion to implement extended agricultural

plantations, especially oil palm. Currently, only ~ 5 % of the land surface is protected to some extent. About half (~ 48 %) of the land area is covered with disturbed forests (Sabah Forest Department, pers. comm.). Our study was conducted in three protected primary rainforests (Kinabalu National Park N 06° 02.248' E 116° 42.482', Tawau Hills National Park N 04°23.974' E 117°53.436', Danum Valley Conservation Area N 04° 57.800' E 117° 48.173') and three secondary forests (Kg. Monggis N 06°13.198' E 116°45.802', Kg. Tumbalang N 06° 08.427' E 116° 53.912', Luasong Field Centre N 4° 36.432' E 117° 23.391'). All of these forest stands comprised >> 1,000 hectares; they were 17 - 236 km apart and situated at altitudes of 200-900 m. The sites in primary rainforest have large numbers of dipterocarp trees rising up to 60 m (e.g. *Shorea spp.*, *Koompasia sp.*) as their prominent cover, usually growing with tree crowns separated from each other. The interconnected and light-shielding canopy occurs at much lower heights between 10 and 40 m. The forest floor is mainly covered by saplings, the dense ground vegetation is mainly limited to patchily distributed treefall gaps and other perturbations. In contrast, sites in secondary forest were 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 (*Dinorchloa spp.*) and other vines, sago palms (*Metroxylon spp.*) and rattan (*Calamus spp.*) which lead to a high structural habitat complexity in the first few meters above ground.

2.3.2 Animal handling and spool application

Our study focused on eight small mammals from the families Muridae, Tupaiidae and Sciuridae (**Table 2.1**). All are common and persist in primary as well as in secondary forests. We classified the species as terrestrial or scansorial (semi-terrestrial, active in the first few meters 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 in 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 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) and marked with subcutaneous transponders (AEG Trovan).

Table 2.1. Studied species, their biometric measurements, and the numbers/ lengths of spools recovered in primary (PF) and secondary (SF) forest. Biometric measurements are given as the mean proportions of hind feet (HF) and tail (T) to head-body length (HB) with one S.D.

Species	<u>Biometric measurements of adults</u>			<u>Spools recovered</u>	
	Weight [g]	HF/HB [mm]	T/HB [mm]	No. in PF / SF	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 tree shrew <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 tree shrew <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 tree shrew <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

A spool-and-line device consisting of quilting cocoons of approximately 120 m nylon thread (Danfield Ltd., U.K.) encased by a heat-shrinking tube (total weight approx. 1.7 g) was glued with cyanoacrylate (Pattex, Henkel, Germany) to the fur on the back of selected individuals. Fur loss and skin irritation caused by the spool had disappeared in animals recaptured about two weeks later.

Cocoon 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 animal release. As initial movements upon release were sometimes influenced by handling, the first 5 – 10 m of track were discarded and recording was started after the first subsequent change in direction.

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 and changes in direction between steps were assessed with a sighting-compass to the nearest two degrees. Threads were followed until they either ran out, or they were broken without continuation, the spools were shed off by the animals, or the habitat was too difficult for further tracking (movements in non-climbable trees and in a few cases movement through extremely dense undergrowth below treefalls).

During tracking, we categorized the undergrowth density from 0 to 1 m height along steps for an area of approximately 1 m left and right of the track in four classes: (1) light (ground barely covered, plant cover < 20 %), (2) intermediate (ground covered typically by saplings/small trees with the litter still visible, 20 % < plant cover < 70 %), (3) dense (litter hardly visible because of high density of saplings and gap vegetation, 70 % < plant cover < 90 %), and (4) very dense (surroundings completely covered by dense vegetation, litter not visible, plant cover > 90 %, typically in forest gaps). For movements of the animals above ground, we additionally recorded type, diameter and maximal height above ground of supportive structures used.

2.3.3 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 along their paths (see **Table 2.2**).

Variables were analysed to compare between species by pooling data from primary forest only or for all forest sites. Differences in habitat use were further analysed between the sites in primary and secondary forest for all species. Because of small sample sizes, *T. gracilis* and *S. lowii* were not considered in most individual-based analyses.

As the scale of measurement allowed us only to evaluate the proportions of values rather than exact measurements, we used non-parametric Kruskal-Wallis-ANOVA and Mann-Whitney-U statistics for all variables. Dunn's test was used for *post hoc* pair-wise comparisons of variables. To evaluate the overall differences of specific paths used by species, we applied factor analysis (FA) to ordinate means of habitat variables for the five most intensively tracked species for the entire utilized habitat and separately for primary and secondary forest. These ordinations allowed for estimating differences between species or populations by reducing the entire set of parameters to two descriptors describing 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.

Table 2.2. Explanations for variables used to distinguish habitat utilization along movement tracks. Analysis of variables was either individual-based (I) or pooled (P) and some variables were analysed with respect to the different above ground classes C1-C4 as indicated.

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	$\sum$ (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)	P
TANGL	Turning angle between consecutive steps	P

2.4 RESULTS

A total of 212 movement tracks comprising a total length of 13,525 m were obtained from approximately 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 the lesser tree shrew, *Tupaia minor*. However, this species was not included in any analysis as it spent a large proportion of its activity in the canopy higher than 10 m. Most individuals climbed up vertical trunks or on vines and other supportive structures straight into the canopy after moving a few meters on the ground and thus proper tracking was not possible. Similarly, *N. cremoriventer* also approached the canopy frequently and 50 % of all trial threads could not further be recovered because they led into the upper canopy. However, although the arboreal activity for *N. cremoriventer* was underestimated in our analysis, the comparisons of its habitat use with other species still provided useful information.

2.4.1 Interspecific variations in movement trajectories

Movement patterns were significantly distinct between species for all variables in multivariate analysis (all Kruskal-Wallis ANOVA $H > 16.27$, $p < 0.05$) (Table 2.3, Fig. 2.1), except for the proportion of movement in medium and very dense undergrowth (UNDENS (2), (4), both Kruskal-Wallis ANOVA $H < 13.6$, $p > 0.05$).

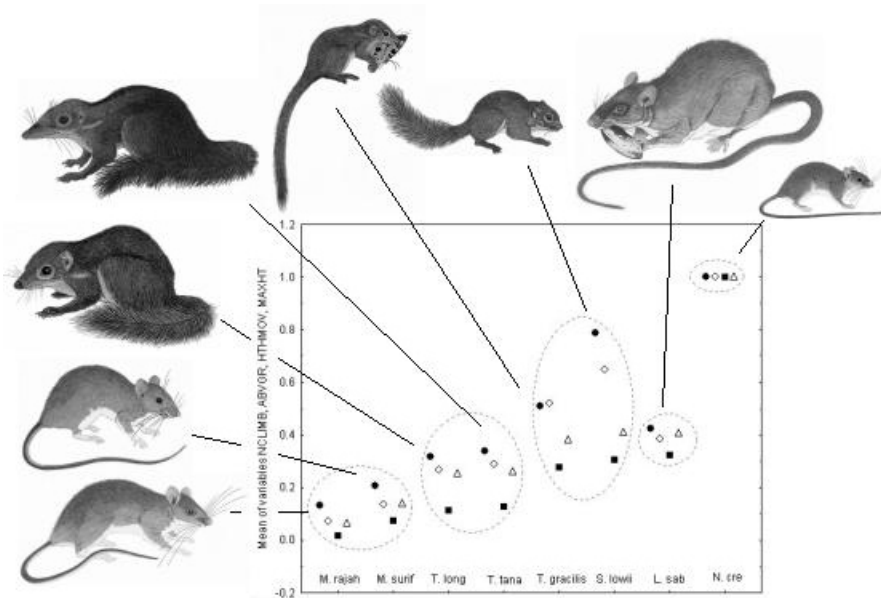


Fig. 2.1. Mean of variables describing the vertical habitat use of the observed small mammal assemblage. The three categories (C1-C3) for the variables NCLIMB and ABVGR were pooled so that the mean of all classes were multiplied by class number and an overall mean was calculated. The variables NCLIMB (●), ABVGR (◊), HTMOV (■), and MAXHT (Δ) are presented for all studied species. Species with a similar habitat use are encircled to demonstrate the different types of vertical habitat utilization found in our study (see discussion). Small mammal illustrations are reproduced from Payne *et al.* (1998) with kind permission from the Sabah Society (Kota Kinabalu, Malaysia).

Post hoc pair-wise comparisons with Dunn statistics revealed 59 variables out of 392 that were significant describing the moving tracks of the eight species. *Niviventer cremoriventer* ($n = 32$), *Maxomys rajah* ($n = 23$) and *Sundasciurus lowii* ($n = 18$) accounted for most of these differences. The closely related species *T. longipes* and *T. tana* as well as *M. rajah* and *M. surifer* did not differ in any of the variables of the pair-wise comparisons.

These patterns of species segregation were also obtained from FA (eigenvalues: $\lambda_1 = 7.08$, $\lambda_2 = 4.27$), for which distances between species were significantly correlated with the number of significant variables between species from Dunn statistics (Spearman's R , $R_{n=28} = 0.72$, $p <$

0.01), indicating that factor analysis accurately represented the extent of habitat segregation across the species. The first FA axis represented a gradient in above-ground activity and explained 44 % of variability in the movement patterns, whereas the second axis explained 27 % of variability of several parameters (**Fig. 2.2**).

Table 2.3. Mean of variables given as values relative to 100 m of the track averaged for all individuals except for the variables DIAM, STEPL, and TANGL, which were calculated as medians for the entire set of specifically pooled data.

Habitat variable	Leo sab	Max raj	Max sur	Niv cre	Sun low	Tup long	Tup tan	Tup grac
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 [°]	46.6	45.4	47.0	60.3	37.1	45.3	46.8	53.6

The diameters of supportive structures generally declined with movement heights (DIAM, Kruskal-Wallis ANOVA $H_{n=974} = 100.12$, $p < 0.01$). Species that climbed more often, moved significantly less in light undergrowth (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 $R_{n=8} = 0.76$, $p < 0.05$) but no correlation was found 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 2.1) 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 $R_{n=8} = -0.93$, $p < 0.01$).

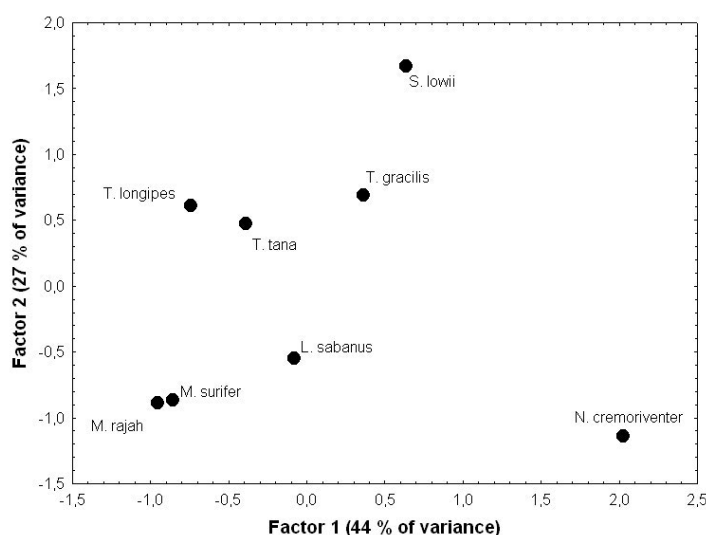


Fig. 2.2. Factor analysis plot of movement patterns of all investigated species based on the means of variables from the entire habitat sampled. The first FA axis represents a gradient in above-ground activity (NCLIMB, ABVGR, HTMOV, MAXHT), whereas the second axis is mostly explained by STEPL, DIAM and LOGMOV. Eigenvalues: $\lambda_1 = 7.08$, $\lambda_2 = 4.27$.

2.4.2 Movement patterns in primary versus secondary forest

All species differed in their movement patterns between primary and secondary forest, with most changes being recorded for *L. sabanus* (Table 2.4). *Maxomys rajah* and *L. sabanus* travelled significantly greater distances at heights of 1 - 50 cm in primary than in secondary forest (ABVGR C1, both M.-W.-U tests $U > 30$, $p < 0.05$). However, whereas these differences in the above-ground movements at this height indicated more above-ground activity for *M. rajah* in primary forest, the opposite was true for *L. sabanus*, which moved on average longer distances (although not significantly) at heights between 1 - 5 m (C3) in

secondary forest and were recorded to climb up in the canopy > 5 m (C4) in three times in secondary forest, but never in primary forest. *Niviventer cremoriventer* climbed more often above heights of 50 cm in primary forest (NCLIMB C2-C4, M.-W.-U test, $U = 8$, $p < 0.05$) and travelled longer distances at heights between 1-50 cm in primary than in secondary forest (ABVGR C1, M.-W.-U, $U = 10$, $p < 0.05$). Whereas *M. rajah* used the above-ground habitat more intensely in primary forest (HTMOV, M.-W.-U, $U = 33.0$, $p < 0.05$) and climbed on average higher up in primary than in secondary forest (MAXHT, M.-W.-U, $U = 27.5$, $p < 0.05$), *T. longipes* used the above-ground habitat more intensely in secondary forest (HTMOV, M.-W.-U, $U = 82.5$, $p < 0.05$). Thus, *T. longipes* and *L. sabanus* revealed an increase in above-ground movement in secondary forest, whereas *M. rajah* decreased in its above-ground activity in secondary forest.

Table 2.4. Intraspecific changes in movement trajectories between primary and secondary forest. The two means as values relative to 100 m of the track (primary – secondary forest) and z-values in parenthesis for all significant differences for means of variables with $p < 0.05$ (M.-W.-U tests) are given. Positive values indicate higher averages for primary forest, whereas blank cells represent non-significant comparisons.

	<i>Leo sab</i>	<i>Max raj</i>	<i>Max sur</i>	<i>Niv cre</i>	<i>Sun low</i>	<i>Tup long</i>	<i>Tup tan</i>	<i>Tup grac</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 primary than in secondary forest (LOGMOV, both M-W-U test $p < 0.05$). The diameter of supportive structures used by *L. sabanus*, *T. longipes*, *T. gracilis*, and *S. lowii* were larger in primary forest (DIAM, for all M.-W.-U test $U > 24.0$, $p < 0.05$) and marginally larger for all other species in primary than in secondary forest. *L. sabanus* moved greater distances in regions with light undergrowth and shorter distances in intermediate undergrowth areas in primary forest (UNDENS, both M.-W.-U tests $U > 170$, $p < 0.05$). *T. tana* moved longer distances in areas with intermediate undergrowth but shorter distances in dense undergrowth in primary than in secondary forest (UNDENS, both M.-W.-U tests $U > 286$, $p < 0.05$). Step lengths were shorter for *L. sabanus* and *T. longipes* in secondary forest, whereas step lengths were longer for *M. surifer* and *T. tana* in secondary forest (STEPL, all M.-W.-U tests $U > 196,291$, $p < 0.01$). Absolute turning angles between steps were smaller for *L. sabanus* in secondary forest (TANGL, M.-W.-U, $U = 206,593$, $p < 0.01$). Analysis of differences of variable means between species and population of the five most intensively studied species in primary and secondary forest by FA (eigenvalues: $\lambda_1 = 5.53$, $\lambda_2 = 4.23$, **Fig. 2.3**) confirmed that changes in movement patterns were most obvious for *L. sabanus*, although all species were affected. Notably, the directions of changes in the resulting multivariate space were of opposite trend for the species *T. longipes* and *T. tana* as well as *M. rajah* and *M. surifer* (Fig. 2.3).

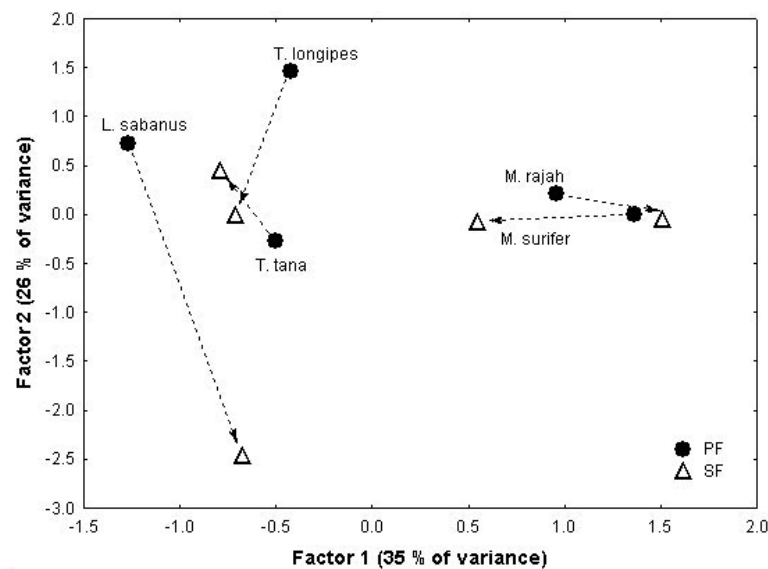


Fig. 2.3. Factor analysis plot of movement trajectories of the five most intensively tracked species in primary (PF) and secondary (SF) forest based on the means of variables. Arrows indicate the direction of changes in movement patterns in multivariate space between primary and secondary forest. The first axis is mainly explained by NCLIMB C2-C4, ABVGR C2 and MAXHT, whereas axis 2 is mainly described by UNDENS (2), HTMOV, and LOGMOV. Eigenvalues: $\lambda_1 = 5.53$, $\lambda_2 = 4.23$.

2.5 DISCUSSION

2.5.1 Interspecific variations in movement trajectories

The segregation of small mammals in tropical assemblages along vertical strata or by body size is broadly considered to favour coexistence among species, with most studies having been conducted in neotropical rainforest sites (e.g. Charles-Dominique *et al.* 1981; Janson & Emmons 1991; Malcolm 1991; Emmons 1995; Voss & Emmons 1996; Bakker & Kelt 2000; Cunha & Vieira 2002). Although less is known about small mammal assemblages in the tropical forests of SE Asia, similar patterns in substrate use have been suggested because of general constraints in climbing ability and adaptation 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. All species showed some scansorial activity and even terrestrial spiny rats (*M. rajah* and *M. surifer*) used the scansorial habitat to some extent. *M. rajah* was the most terrestrial species with only 10 out of 23 individuals (43 %) leaving the ground at heights of less than one meter. The two larger tree shrews *T. longipes* and *T. tana*, which have been mainly described as terrestrial based on field observations (Emmons 2000) and morphological traits (Sargis 2001a, b), revealed greater climbing activity than spiny rats, with half of all of their tracks reaching heights of 1 meter or above. 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 or substrates (Emmons 2000). Therefore, long-distance movement (with regard to our findings) and foraging may take place in different microhabitats and the utilization of resource patches and inter-patch movement may be independent of each other for these species.

We confirmed the occasional arboreal activity of *L. sabanus* in our study, although this species spends proportionally much more time on the ground than the scansorial species *S. lowii* and *T. gracilis*. We might have underestimated the arboreal activity of *L. sabanus* because we could not follow threads into the arboreal habitat. Indeed, trapping activity at the same and other localities has confirmed that this rat might climb regularly above heights of 10 m, particularly in secondary forests (pers. obs.; see also Lim 1970; Wells *et al.* 2004). The underestimation of arboreal activity in our study attributable to methodological constraints was most severe for the rat *N. cremoriventer*, which spends a large proportion of its activity in the upper canopy. Nevertheless, our data provide support for the hypothesis of species

stratification. The distinct vertical movement patterns were similar to those noted for mammal assemblages in the neotropics (see Charles-Dominique *et al.* 1981; Voss & Emmons 1996; Cunha & Vieira 2002). Our results revealed for the local assemblages on Borneo terrestrial species (*M. rajah*, *M. surifer*), species that were mostly active on the ground but occasionally reached the upper canopy (*L. sabanus*), terrestrial species with frequent scansorial activity (*T. tana*, *T. longipes*), scansorial species that were not active in the canopy (*T. gracilis*, *S. lowii*) and, finally, arboreal species that approached occasionally the ground (*N. cremoriventer*, *T. minor*). In contrast to studies at neotropical sites, climbing activity of small mammals was not related to body size but rather to morphometric measurements (HF/HB and T/HB), indicating that species of variable sizes are adapted to cursorial versus arboreal activity. Although some convergences between small mammals assemblages have been reported for the neo- and paleotropics (see Emmons 1995), vertical patterns in body-size distribution can not necessarily be expected to be equivalent. It has been suggested that arboreal vertebrates in the neotropics are in general smaller than paleotropical vertebrates because of the relatively more fragile canopy structure in that region (Cristoffer 1987) and the differences in morphological modifications such as gliding that occurs predominantly in the paleotropics or prehensile tails that are prevalent in the neotropics, which may in turn affect the accessibility and use of vegetation structures (Emmons & Gentry 1983). On the other hand, neotropical assemblages of small mammals that included only small numbers of species under investigation have usually been described with the inclusion of some larger bodied (mostly terrestrial) didelphids, such as *Didelphis spp.* (weights above 1 kg) or *Metachirus spp.* (weights above 500 g; see Wilson & Reeder 1992, references above) that might bias the conclusions on body size distribution drawn from these assemblages.

Interestingly, habitat segregation was weak between the two pairs of species in our model: *M. rajah* versus *M. surifer* and *T. longipes* versus *T. tana*. Both pairs of species exhibit paraphyletic relationships (Ruedas & Kirsch 1997; Han *et al.* 2000), indicating that their similar morphological appearance and body size are convergent adaptations to their ecologically similar niche. In contrast, the two smaller tree shrews *T. gracilis* and *T. minor*, which also exhibited substantial convergence in body size and morphology (Han *et al.* 2000), use distinct habitats along the vertical axis. Whereas *T. gracilis* is confined to the scansorial layer, *T. minor* is active in the upper canopy with occasional descents to the ground.

If rainforest mammals partition resources vertically, 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 energetic constraints along the vertical axis. Although we have learned over the past decade, that complex rainforests support convergent syntopic species in similar ecological niches, the way partitioning functions on such a fine spatio-temporal level for such species remains to be investigated.

2.5.2 Movement patterns in primary versus secondary forest

One reason that species occur in particular sets of habitats are their adaptation to preferred habitats. 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 rainforest environment. We found little evidence that any of the investigated species was restricted to a single set of structural habitat type, although our trapping success was not homogeneously distributed through space and time for any species (**Chapter 1**). *Sundasciurus lowii* and the smaller tree shrews *T. gracilis* and *T. minor* were usually trapped more patchily than other species. All of the most commonly trapped small mammals in the local rainforest areas persisted in logged forests. Our comparisons of movement trajectories of the animals between primary and secondary forests clearly showed that highly modified forest structures in secondary forests with denser undergrowth, low sapling densities and reduced canopies affected the movement trajectories of all investigated species. The observed shifts in movement trajectories might result from (1) the altered structure per se, (2) changes in vertical partitioning of resources (e.g. Cunha & Vieira 2002) or (3) differences in spatial orientation and environmental perception by the species attributable to different habitat structures (e.g. Grobety & Schenk 1992; Jacobs & Shiflett 1999). As the response of the individual species to habitat alteration was very variable, changes in habitat structure and their effects on small mammals are difficult to interpret when a single species is examined. This requires the evaluation of the entire set of different focal species for a given habitat type. Some general shifts in habitat use become evident when we consider the most severe habitat change, here the reduction of canopy space and structure attributable to the extraction of emergent trees in logged forests. As a consequence, arboreal species and biomass may shift from the canopy to the ground in secondary forests (Malcolm 1997; Struhsaker 1997). Furthermore, differences in branch textures may alter interconnected movement tracks of animals (see Malcolm 1995). Both, terrestrial and scansorial species are encountered in secondary forest with denser undergrowth and more scansorial supportive structures that may influence movement; however, the prediction of shifts in vertical movement patterns in response to these habitat differences is

less evident, as species might quickly change between the two neighbouring habitat layers (ground vs. understorey supports) and pay-offs (e.g. microclimate) between these layers might be less stringent than for the terrestrial-arboreal dichotomy.

A general difference of movement trajectories between the two habitat types was only found for the diameter of utilised structures, which declined in secondary forests for all species. Apparently, this general pattern referred to an overall change in branch diameters rather than to any particular preferences of the small mammals for any supportive structure. There were, for example, fewer large logs or thick arboreal branches in secondary forests, whereas the abundance of thin supports increased in the understorey particularly because of the fast growing and highly abundant climbing bamboo, *Dinochloa spp.*, with diameters between 1-3 cm, which are frequently used for climbing by various species (pers. obs.). Smaller climbing mammals might profit from thin supports (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 secondary forests for any particular species or the entire assemblage remain unclear. For example, *L. sabanus*, the largest focal species, frequently used thin supports (ca. 20 % of used supports ≤ 2 cm) and showed increased climbing activity in secondary forests, whereas the climbing activity of the much smaller *N. cremoriventer* was reduced in secondary forests, despite this species showed in general a clear preference for small diameters (Table 2.3). 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 secondary forests. Only *T. tana* and *L. sabanus* moved longer distances in dense undergrowth in secondary forests. Diurnal tree shrews might profit from dense ground cover as a strategy for predator avoidance (Emmons 2000) as they generally moved greater distances in dense undergrowth than nocturnal rats (Table 2.3). Although this strategy has been suggested for several tropical small mammals (e.g. Emmons 2000; Lambert & Adler 2000; Vernes 2003; Wells *et al.* 2004) it needs to be tested with behavioural experiments and with further information with respect to associated geometric, abiotic and biotic habitat features.

Little is known about such differences between primary and secondary forests. Studies comparing small mammals in undisturbed forests and the tree-fall gaps therein indicate that various influential factors 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 and references therein). The

arguments so far lead to the conclusion that any particular habitat change such as structural differences between primary and secondary 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 can be most comprehensively analysed in a multivariate approach. Our analysis suggests that specific movement patterns are differently affected in secondary forests where most variability between species is explained by variables related to climbing activity (see Fig. 2.3). We did not detect any trends in shifts of movement patterns with regard to characters such as body size, taxonomic grouping or vertical guilds. Further, no common tendencies were seen in the shift of movement trajectories for congeneric species such as *M. rajah* and *M. surifer* or *T. longipes* and *T. tana* despite their strong convergence and similar 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 are able to persist in disturbed forest habitats, although other studies suggest that more specialized species react negatively to environmental variability (e.g. Henein *et al.* 1998; Purvis *et al.* 2000; Harcourt *et al.* 2003). This might also be of relevance for some rare and less well-known species in the Bornean assemblage. 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 of these little known species. However, an improvement of our appreciation of the way that species react in their movement patterns to habitat disturbance might provide a promising approach to understanding the ecological basis of interspecific variation in the adaptability, decline and persistence of tropical rainforest mammals. The inconsistency in logging responses suggest that it is not possible to broadly apply knowledge of how a particular species is affected by logging to others, underlining the importance of species-based approaches in understanding the effects of habitat degradation in speciose assemblages.

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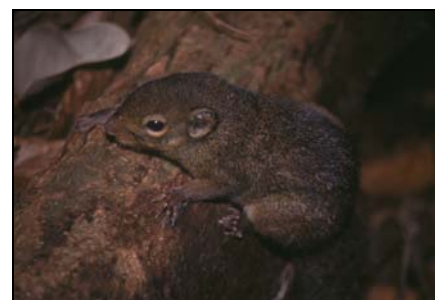
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Top left to bottom right:

- Spool application to *Tupaia tana*.
- Following an uncoiled thread.
- Nest from *Niviventer cremoriventer*.
- *N. cremoriventer* moving on a branch.
- Juvenile *N. cremoriventer* after emergence from nest.
- Thread leading into a borrow from *Maxomys rajah* (entrance closed with a leave).
- Thread leading into a burrow from *Tupaia tana*.
- *Maxomys rajah*.
- *Sundasciurus lowii*.



Movement and ranging patterns of a tropical mammal, the long-tailed giant rat (*Leopoldamys sabanus*), in primary and secondary rainforests on Borneo

3.1 ABSTRACT

The movement paths of animals are integral features of the environment. Knowledge of the way in which organisms move through landscapes is thus important for predicting effects of habitat structure and resource availability on wildlife distribution and habitat utilisation. Rainforest logging results in a suite of habitat differences that may modify movement of animals at various scales in response to altered structure and resources.

Movement and ranging patterns of the generalist long-tailed giant rat *Leopoldamys sabanus* were investigated in primary and secondary rainforests on Borneo (1) on a small scale by spool-and-line tracks and (2) on a larger scale by radio-tracking. At the small scale (49 tracks of 55.2 ± 20.7 m), paths were relatively straightforward with shorter straight-line sections (step lengths) in secondary than in primary forest. The similarly large proportion of relatively short step lengths in both forest types did not fit a normalized probability distribution, allowing us to reject random walk models as assumed for random movements with constant step lengths in homogeneous landscapes. On the larger scale (16 radio tracks of four nights, averaging $1,443 \pm 991$ m per night), movement lengths during 10-min intervals were described by similar power-law distributions for both forests types with a mean distance of 32.09 ± 44.85 m travelled.

Significant serial correlation in consecutive movement lengths (Spearman $R > 0.13$, $p < 0.01$) and spatial autocorrelation in geographical positions along subsequent movement steps as analysed by Mantel statistics (26 out of 64 nightly paths with $p < 0.05$) suggested that rats conducted concentrated search efforts with sequent short moves in some patches. The mean nightly activity

periods of 485 ± 109 min resulted in ranges between 535 to 8,987 m² (95 % kernel estimates). Our data showed no common patterns at the two scales. The large variability in movement parameters among individuals was neither predicted by sex nor forest type, suggesting that paths were local responses to adjustments of movement and the location of resources in a heterogeneous complex rainforest environment. Logged forest may therefore retain many features relevant to movement and ranging patterns of generalist mammals such as *L. sabanus*.

3.2 INTRODUCTION

The decision rules that determine foraging strategies or other types of movement of animals are given by environmental features that are perceived by animals and responded to for effective locomotion and resource localization. The various resources that animals search for during movement (e.g. food, mate, shelter) serve as antagonistic components in an interaction-diffusion process, in which a forager's motion and resource encounter are determined by both the medium/environmental conditions and the distribution of resources therein. Thus, the optimal search strategy is a central theme that focuses on how to maximize encounter rates of resources in complex landscapes (Shlesinger *et al.* 1993; Viswanathan *et al.* 1996). Since complex landscapes such as speciose tropical rainforests are patchy and resources are often distributed in nested patch hierarchies (MacArthur 1972; Solé & Manrubia 1995), the manner in which animals encounter and use such environments at various scales has gained considerable interest (Wiens 1989; Benhamou 1990; Kotliar & Wiens 1990; With 1994; Ritchie 1998; Johnson *et al.* 2002; Fauchald & Tveraa 2003; Fritz *et al.* 2003). The tortuosity of paths towards targets is obviously linked to landscape heterogeneity in which obstructions have to be avoided and supports, for instance branches on which non-volant mammals move through the rainforest, are diffusely distributed. The more efficient movement is possible, for instance in an obstacle-poor habitat with numerous resource patches, the more should a path represent a straight line between the starting and the respective target. In this context, the resolution of path tortuosity depends on the specific perceptual range of the moving animal and the extent of environmental heterogeneity. Both may vary and thus influence movement patterns of an animal across a hierarchy of spatial scales (With 1994; Zollner & Lima 1997). The scale of sampling to delimit the path of an animal is of much importance here: whereas a fine-scale resolution will give the most realistic results,

meaningful autocorrelation effects among subsequent moves are lost and movements will appear to be more random by increasing sampling length (Turchin 1998; Cushman *et al.* 2004). In contrast to small-scale assessment of movement patterns, quantification of movement patterns and path tortuosity on larger scales is a valuable approach to investigate the distribution and quality of patches in a landscape. For example, increased resource abundance in patches may result in shorter movements and more frequent turns as a response to increased resource intake (e.g. area-restricted search, Walsh 1996; Grünbaum 1998). Conversely, crossing of suboptimal habitat patches or extensive search movements should be characterized by straight-line movements and small turning angles.

To gain a better understanding how animals interact with their environment on various scales is not only a matter of selecting a proper scale and recording method for analysis, but also of how to meaningfully describe these interactions by modelling particular movement trajectories of the animal. Over limited time scales, the description of movement patterns by a diffusion equation modified from Brownian motion with the assumption of a Gaussian step-length distribution of the independent steps has been successfully used in predicting dispersion (Kareiva & Shigesada 1983; Turchin 1998). However, such models are based on the assumption of a landscape with even distribution of resources and do not take structural components into account, such as the uneven distribution of trees and resources in a heterogeneous rainforest matrix (Condit *et al.* 2000). In such case, Lévy walk patterns with a broad distribution of long straight-line movements interrupted by localized random motions (see Shlesinger *et al.* 1993; Klafter & Sokolov 2005) have been successfully applied to vertebrate movements in heterogeneous landscapes with unpredictable or patchy resource distribution (Viswanathan *et al.* 1996, 1999; Atkinson *et al.* 2002; Mårell *et al.* 2002; Ramos-Fernández *et al.* 2004). Lévy walk processes not only predict a forager's response to patchily distributed or spatially aggregated resources, but also incorporate scaling relationships that predict a fractal-like and nested behaviour of movement features over a large range of spatial (or temporal) scales. Such self-similar scaling patterns have been empirically reported both for foraging strategies (Ritchie 1998; Haskell *et al.* 2002) and underlying habitats (Solé & Manrubia 1995; Gisiger 2001; Brown *et al.* 2002).

In this context, tropical rainforests provide a challenging habitat for modelling animal movements. The outstanding diversity of tropical forest trees, which largely determine overall habitat structure and resource distribution and provide three-dimensional complex pathways for animals, offers a notable framework for studying the function of ecosystems in relation to

physical structure and diversity (Richards 1996). Tropical trees and their associated flora and fauna occur in a variety of numbers and degrees of aggregation (Condit *et al.* 2000), such that some species are available to many potential consumers and others only to a few. Consequently, some resources may be unevenly distributed among patches. Gaps that comprise a central element in maintaining rainforest diversity and resource distribution (Hubbell *et al.* 1999) occur in a fractal-like fashion (Solé & Manrubia 1995). Such compositional and physical features suggest that Lévy walk tactics are more efficient in exploring this environment than Brownian dispersal strategies (Solé *et al.* 2005), as has been found for the movement patterns of spider monkeys *Ateles geoffroyi* in Mexican rainforests (Ramos-Fernández *et al.* 2004). Tropical tree diversity and the resulting resource distribution have also been found to influence spacing patterns of the generalist neotropical rat *Proechimys semispinosus* (Adler 2000), suggesting that the principles of aggregation and scale may be applicable to species that are tolerant to variable patch properties by definition.

Particularly with respect to generalistic and wide-ranging species, different movement models may apply for a single species because of interspecific variability in foraging strategies or behavioural states as a response to environmental variability (Austin *et al.* 2004; Morales *et al.* 2004). Furthermore, movement strategies may be altered in environments with different patch characteristics such as size and resource distribution within patches (With *et al.* 1999; Zollner & Lima 1999). The rapid destruction of rainforest attributable to timber harvesting and agricultural land use adds a considerable component of habitat variability to tropical environments, with as yet unforeseeable consequences for wildlife species. Logged tropical rainforests do not only differ from primary forests in terms of floral composition, but also in the scale of habitat heterogeneity, as patches in secondary forests contain fewer species of large trees and require a larger area for enclosing the same number of tree species than primary forests (Cannon *et al.* 1998). Moreover, evidence is increasing that the effects of forest degradation on species performances and dynamics are strongly scale-dependent (Condit *et al.* 2002; Hill & Hamer 2004). For example, studies of birds conducted at large spatial scales were more likely to report increased diversity, whereas studies that sampled habitats at small spatial scales were more likely to report decreased diversity in disturbed rainforests (Hill & Hamer 2004). Animals that move in secondary rainforests thus encounter differences in structure (e.g. more dense undergrowth in combination with a reduced canopy and more gaps) and resource allocation (e.g. different plant material attributable to changed floral composition) (e.g. Uuttera *et al.* 2000; DeWalt *et al.* 2003)

than the same species in primary rainforest. Those differences may affect movement strategies within species.

Studies focussing on the variability of movement at different scales have shown that different environmental features may constrain movement at different scales (Rettie & Messier 2000; Johnson *et al.* 2002; Fauchald & Tveraa 2003; Fritz *et al.* 2003; Nams & Bourgeois 2004). Hence, it is important to understand the reasons of those discrepancies in order to be able to project movement trajectories determined at one scale onto a larger scale.

In the present study we investigated movement and ranging patterns of the long-tailed giant rat *Leopoldamys sabanus* at two spatial scales by using both spool-and-line and radio-tracking in primary and secondary rainforests in Borneo. This large forest rat is present in many primary and secondary forest sites throughout the Sunda region in SE Asia and comprises a common species in local assemblages of small mammals (Musser & Carleton 1993). It consumes a variety of animal and plant material (Liat 1970). Giant rats are mostly active on the ground with occasional forays up into the canopy. They have been observed to move a larger proportion of their path above ground in secondary forests than in primary forests (**Chapter 2**). Furthermore, whereas the diameters of structural supports such as branches utilized by these rats are smaller in secondary forest, logs are more frequently used as pathways in primary forest (**Chapter 2**). We therefore hypothesized that the different physical structure in secondary forest should lead to further differences in small-scale geometric path trajectories. Because giant rats are also likely to respond strongly to changes in resource abundances and distribution in primary and secondary forest, we further hypothesized that variation in forest characteristics may also lead to differences in movement and ranging behaviour on a larger scale. We additionally record on burrows found with either observation method.

3.3 METHODS AND MATERIALS

3.3.1 Study sites

The study was conducted in three primary and three secondary forest sites in northern Borneo (Sabah, Malaysia) between December 2002 and November 2004. Sites in primary forest comprised some of the few remaining larger remnants of primary lowland rainforests composed of dipterocarps that have been gazetted as national parks or conservation areas (Poring, Kinabalu

NP at 06° 02.248' N, 116° 42.482' E; Tawau Hills NP at 04°23.974' N, 117°53.436'E; Danum Valley Conservation Area at 04° 57.800' N, 117° 48.173' E). Study sites in secondary forest sites were in areas that had been selectively logged 20 –30 years previous to our study with most dipterocarp and other larger trees having been extracted (Kg. Monggis at 06°13.198' N, 116°45.802' E; Kg. Tumbalang at 06° 08.427' N, 116° 53.912' E; Luasong Field Centre at 4° 36.432'N, 117° 23.391' E). Details on the logging histories for the study sites were not available, but all secondary forest stands differed considerable from primary forests with reduced canopy heights (approximately 15-25 meters), frequent gaps and denser undergrowth than in primary forest.

3.3.2 Capture and tracking techniques

Rats were captured between September 2002 and November 2004 with locally made wire-mesh cage traps baited with banana in 18 trapping sessions that were conducted consecutively at the various study sites (**Chapter 1**).

A spool-and-line-device consisting of quilting cocoons of approximately 120 m nylon thread (Danfield Ltd., U.K.) encased by a heat-shrinking tube (total weight: approx. 1.7 g) was glued with cyanoacrylate (Pattex, Henkel, Germany) to the fur on the back of selected individuals. The free end of the thread was tied to nearby vegetation and labelled. The threads were usually tracked the day following the release of the animal. We used plastic poles to the sections where the tracked animal had walked without recognizable change in direction or change in recorded habitat characteristics. These sections ('step lengths') were measured with a measuring tape to the nearest 0.1 m. Changes in direction between steps were recorded with a sighting-compass to the nearest two degrees. Further details and results regarding habitat features along paths have been published elsewhere (**Chapter 2**).

Suitable individuals were fitted with radio collars (Biotrack, U.K.), which broadcasted at 150 MHz and weighed less than 3 % of the body mass of a giant rat. This is less than the 10 % mass threshold above which transmitter mass is regarded to seriously affect an animal's foraging behaviour (Brander & Cochran 1969). As tracked rats were located in a complex environment with solid canopy coverage and a paucity of nearby footpaths, early attempts to establish reference points with a satellite-based positioning system (Garmin 12, Garmin Ltd.) were discarded. Instead, we selected starting points in a suitable terrain close to presumed ranging areas and established further reference points marked with plastic poles by using compass

bearings and by measuring tape distances. To facilitate quick movements of the principle investigator between reference points within approximately 1 minute, dense undergrowth vegetation was removed between points.

Individual rats were tracked for at least four consecutive nights from dusk (starting between 1700 h – 1830 h) until they returned to their den (continuing tracking for about two hours of inactivity of the rat or until dawn at approximately 0500 h) with regular time periods of 10 min between successive recordings. Recordings were made by using a hand-held Yaesu VR-500 receiver (Yaesu Musen Co. Ltd., Japan) with a modified hand-held H-aerial antenna (Wagener Telemetrieanlagen, Germany). The small size of this equipment proved to be essential for tracking in dense vegetation; an early attempt with a 3-element yagi antenna (Wildlife Materials Inc., Illinois, USA) was unfeasible in most study sites. The hilly terrain and vegetation made tracking in close proximity to the ranging areas of rats necessary and limited the accuracy of triangulation bearings to an estimated error of 10-30 m. Although some rats were occasionally spotted near reference points, there was no noticeable impact on their movement patterns. Rats were recaptured afterwards and, whenever possible, radio collars were retrieved. One rat that is not included in the analysis was found dead a few days after application of the collar; we were not able to identify the cause of its death as there was no obvious impact from the collar.

3.3.3 Data analysis

Movement paths on both examined scales are represented by discrete positions of the tracked animal and straight distances moved between consecutive points. These comprised mathematically a vector with a turning angle. Although step/movement lengths and turning angles do not necessarily have a biological meaning, they are basic features for the analysis of paths. Consecutive locations can thus be connected by straight lines to approximate paths on the examined scales (**Fig. 3.1, 3.2**).

Locations of rats from radio-tracking were calculated with a maximum likelihood method based on synchronous bearings by triangulation from 10-min intervals with application of the software LOAS (version 3.0.3, 1998 – 2005, <http://www.ecostats.com/software/loas/loas.htm>, Ecological Software Solutions,). For analysis, we considered all fixes taken from the time of emergence from the burrow until the rat either returned to the burrow for resting or until tracking activity was terminated at approximately 0500 h. Some tracking nights were ended earlier because of injury or overfatigue of the investigator. For analysis, we excluded outliers that lay far away

from all other tracked points (> 100 m) and comprised distances > 200 m to neighbouring bearings.

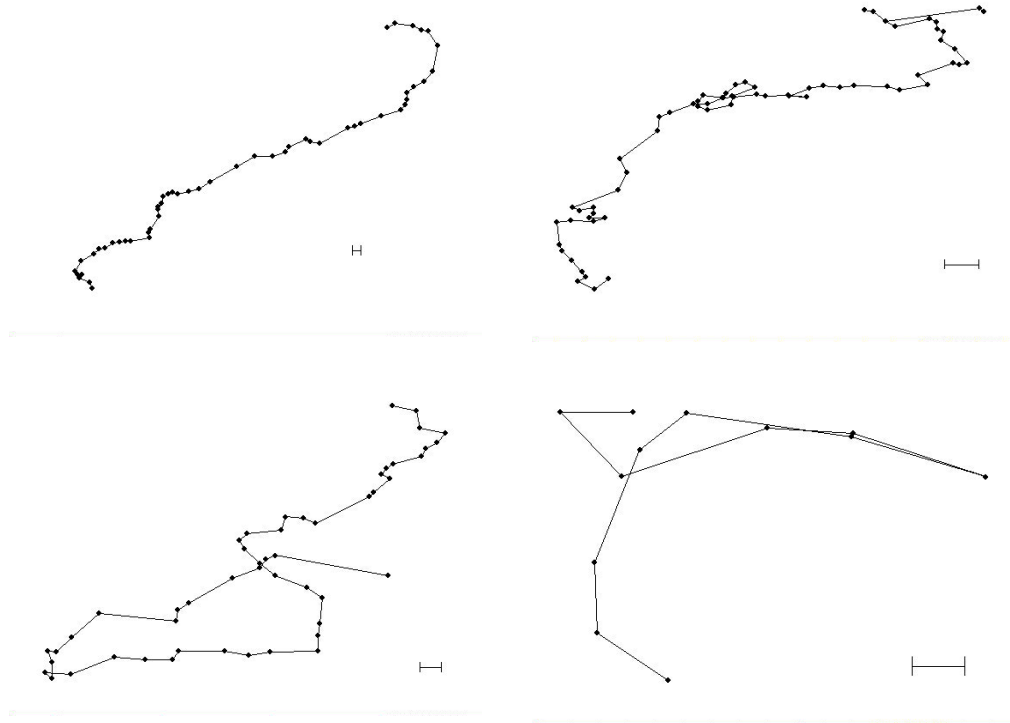


Fig. 3.1. Small-scale movement tracks of four giant rats obtained by spool-and-line tracking. Scale bars represent 1 meter. All tracks except that bottom left are from primary forest.

For movement analysis, distances from radio-tracking data ('movement length') were analysed with a bin size of 5 m from 10-min (± 1 min) intervals, whereas distances from spool-and-line data ('step length') were considered with a bin size of 0.1 m. The frequency distributions of movement and step lengths were tested for an inverse square power-law distribution by using a log-log regression in order to test for different movement models (Turchin 1998; Viswanathan *et al.* 1999). For this, we pooled data among forest types or sex and applied a Student's *t*-test for testing differences in regression slopes (Zar 1999). Means of turning angles were calculated as circular means (Zar 1999). To assess whether turning angles were uniformly distributed with a mean turning angle of $\alpha = 0$, as would be expected for a correlated random walk, we used Rayleigh's circular statistic to test the null hypothesis that the distribution of turning angles was random (Batschelet 1981).

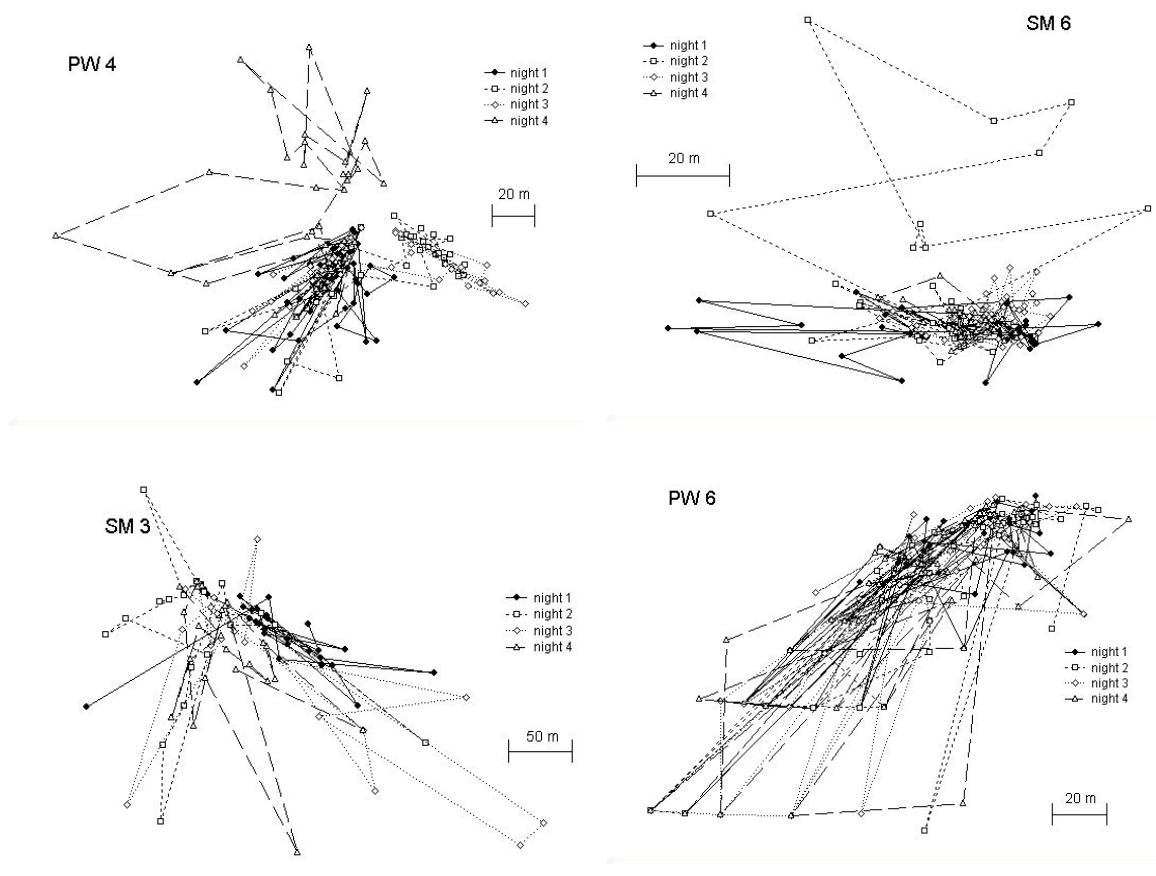


Fig. 3.2. Large-scale movement paths of four giant rats obtained by radio-tracking during four consecutive nights.

We tested movement paths for possible relationships of geographical distances between point estimates of a path with temporal distances between these points using Mantel statistics (Mantel 1967). In this context, the Mantel correlograms represent the extent of spatial autocorrelation in a movement path (see Cushman *et al.* 2005). Straight-line movements should thus reveal a high correlation, whereas a tortuous path should show less correlation.

The utilized ranges were calculated as fixed kernel ranges (Worton 1989) at the 95 % ('total range') and 50 % ('core range') utilization levels, by using least squares cross validation (LSCV) for estimating the smoothing factor. Despite some recent concern regarding these estimates (e.g. Hemson *et al.* 2005), fixed kernel estimators by using LSCV provide currently the least biased and most accurate measurement of range sizes (Seaman & Powell 1996). Calculations of range use were performed with BIOTAS software (Version 2.0, Ecological Software Solutions).

Because we employed fixes at regular time intervals, we assumed that movement and ranging behaviour were most realistically described by the entire data set and considered the inherent autocorrelation as an ecologically informative trait (see De Solla *et al.* 1999; Cushman *et al.* 2005). We were unable to simultaneously examine for possible effects of logging treatment and sex on movement patterns because of small sample size. Instead, we analysed our data separately for both parameters. In order to estimate the variation within consecutive measurements from individual paths, we used the coefficient of variation ($CV = S.E./mean * 100$) to quantify variability within samples and ANOVA to distinguish means. Means are given as ± 1 S.D.

3.4 RESULTS

We obtained a total of 49 spool-and-line tracks of > 30 m (mean 55.2 ± 20.7 m, total: 2,704 m) for 25 individuals that were tracked in primary forest and 24 individuals that were monitored in secondary forest. Sixteen different radio-tracks of at least four consecutive days were recorded, including nine records from primary forests and seven records from secondary forests with a total of nine males and seven females being tracked, respectively (**Table 3.1**). We obtained 2,829 fixes (mean 177 ± 44 per individual) for analysis. Another three trials were excluded from analysis, as the transmitter fell off or were gnawed off before completion of the tracking period.

3.4.1 Small-scale movement patterns

Mean step length from spool-and-line movements was significantly shorter in secondary forest with 1.7 ± 1.2 m than in primary forest with 2.2 ± 1.5 m (t-test, $t = 7.37$, $p < 0.01$). Step-length distribution did not correspond to a probability distribution that could be normalized, with all regression slopes $0.87 < \mu < 1.09$ (all $r^2 > 0.40$) (**Fig. 3.3**). The frequency distributions of short and long steps did not differ among forest type or sex (both Student's t-test $t_{v \geq 115} < 0.92$, $p > 0.20$), indicating that movement trajectories were similar in both forest types despite the shorter step lengths in secondary forests. Serial correlation of step lengths with the previous and the two precedent steps was detected in 3 out of 49 spool-and-line tracks (all Spearman R , $R > 0.31$, $p < 0.01$). Step lengths were positively correlated with turning angles in one spool-and-line track ($R = 0.79$, $p < 0.01$), whereas a negative correlation was obtained in six tracks (all $R < -0.35$, $p < 0.05$).

Table 3.1. Basic results and individual estimates from radio-tracking data for all giant rats (*Leopoldamys sabanus*) tracked during four consecutive nights. The tracks PM2 and PM3 were from the same individual tracked with an eight-month time difference and considered as independent tracks in the following analysis. PF: primary forest, SF: secondary forest.

Individual ID	Sex/ Age	Study site	Date of tracking	Number of fixes taken	Mean nightly path length [m]	Mean nightly ranges (95 % Kernel) [m ²]	Mean activity time [min]
PM 1	Male, adult	PF (Dan)	Dec '03	168	1,550 ± 749	1,297 ± 1,078	525 ± 70
PM 2	Male, adult	PF (Taw)	Sept '03	167	1,339 ± 175	2,135 ± 1,758	420 ± 73
PM 3	Male, adult	PF (Taw)	May '04	195	1,171 ± 136	535 ± 6	495 ± 87
PW 4	Female, immature	PF (Dan)	Dec '03	227	1,342 ± 289	2,048 ± 1,422	590 ± 18
PW 5	Female, adult	PF (Por)	Dec '02	112	1,582 ± 234	555 ± 24	453 ± 54
PW 6	Female, adult	PF (Por)	Jun '03	235	4,742 ± 1,085	734 ± 388	610 ± 42
PW 7	Female, adult	PF (Por)	Jun '03	225	2247 ± 508	535 ± 2	603 ± 52
PW 8	Female, adult	PF (Por)	Feb '04	147	702 ± 261	674 ± 220	395 ± 87
PW 9	Female, adult	PF (Taw)	Aug '03	164	723 ± 212	1,782 ± 1,165	410 ± 29
SM 1	Male, adult	SF (Luas)	Apr '03	100	768 ± 401	1,867 ± 1,549	327 ± 140
SM 2	Male, adult	SF (Luas)	May '04	194	1,823 ± 366	2,708 ± 2,510	495 ± 45
SM 3	Male, adult	SF (Mong)	May '03	104	1,205 ± 264	2,891 ± 2,171	313 ± 69
SM 4	Male, adult	SF (Tumb)	Jul '03	218	618 ± 231	865 ± 239	573 ± 61
SM 5	Male, adult	SF (Tumb)	Mar '04	181	1,521 ± 235	2,827 ± 4,115	458 ± 46
SM 6	Male, adult	SF (Tumb)	Nov '04	191	757 ± 337	1,336 ± 747	527 ± 39
SW 7	Female, adult	SF (Tumb)	Jul '03	223	1,005 ± 360	1,144 ± 750	570 ± 70

The mean turning angle from spool-and-line data was $8.56 \pm 7.81^\circ$ in primary forest and $9.32 \pm 11.27^\circ$ in secondary forest. Directional bias was observed in 33 out of 49 (67 %) spool-and-line tracks (all $n = 33$ Raleigh's $z > 0.322$, $p < 0.05$) with the same frequencies for primary and secondary forest (Chi²-test, $\chi^2 = 0.003$, $p = 0.95$), meaning that most individuals moved with persistence in a particular direction. All spool-and-line tracks showed significant correlations

between geographical displacements and time lags (all Mantel test $p < 0.01$) and comprised relatively straight-line movements (Fig. 3.1). However, spool-and-line tracks revealed also considerable variation as indicated by relatively large CVs for variables (**Table 3.2**).

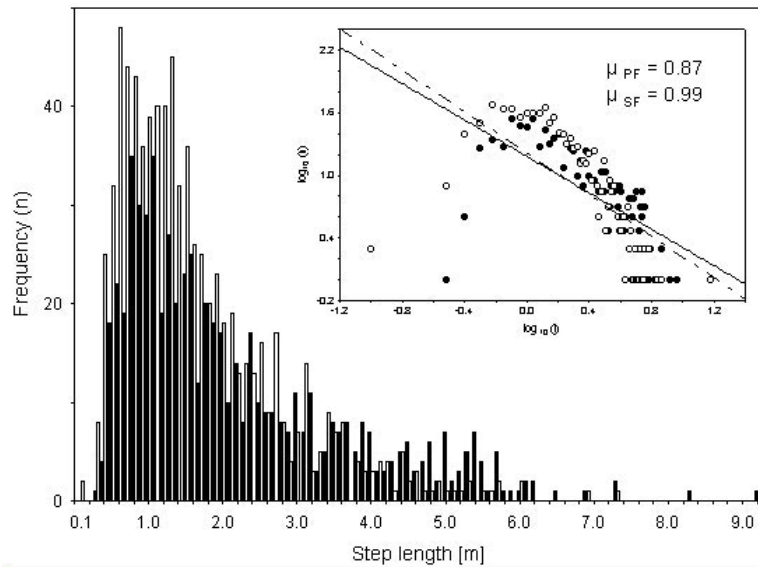


Fig. 3.3. Distribution of step lengths from spool-and-line tracking of giant rats moving in primary (PF, black) and secondary forest (SF, white). The inset shows a log-log plot of the same data fitted with regression lines (both $r^2 > 0.56$) with $\mu = 0.87$ for primary forest and $\mu = 0.99$ for secondary forest not significantly different (Student's t -test $t_{v=119} = 0.80$, $p > 0.20$). Estimates are based on a bin size of 0.1 m with $n = 629$ steps for primary forest and $n = 795$ steps from secondary forests. Values of $\mu \leq 1$ do not correspond to a probability distribution that can be normalized.

3.4.2 Large-scale movement patterns

The mean distances travelled during a single night were $1,443 \text{ m} \pm 991 \text{ m}$ with no differences among sex or forest type (both t -test $t < |1.25|$, $p > 0.23$). The longest recorded average distance per night was $4,742 \pm 1,085 \text{ m}$ covered by a female (PW6), whereas the shortest movement per night was $618 \pm 231 \text{ m}$ recorded for a male (SM4). A total of 2,432 movement lengths from 10-min intervals with a mean distance of $32.09 \pm 44.85 \text{ m}$ were obtained. Movement lengths were significantly shorter in secondary forest than in primary forest and shorter for males than for females (both t -test $t > 5.17$, $p < 0.01$) when all measurements were considered. These differences were not obvious any more when comparing the mean movement lengths from

individuals. Mean movement lengths were significantly distinct among individuals (ANOVA, $F_{15,48} = 9.33$, $p < 0.01$), indicating that the large variability among individuals might blur any logging effects on movement patterns.

Table 3.2. Variation in small-scale paths from spool-and-line tracking. Minimum and maximum means from tracks are given. CVs are presented to indicate the variability among all tracks. Spearman's R correlations with $p < 0.05$ between variables are represented by their respective abbreviations.

Variable		Min. – Max. Means	Correlations	CV [%]
Step length [m]	(SL)	1.1 – 4.8	RR	153.0
Turning angle mean [°]	(β)	0.19 – 48.46		59.0
Raleigh's R	(RR)	0.13 – 0.90	SL, Mr	45.1
Mantel r	(Mr)	0.98 – 1	RR	23.3

The movement-length distributions during 10-min intervals resembled Lévy walk distributions (**Fig. 3.4**) with similar slopes of the log-log regressions (all $r^2 > 0.78$) among forest types and sexes (all $1.45 < \mu < 1.74$, Student's t-test for forest type $t_{v=88} = -0.62$, $p > 0.50$, for sex $t_{v=90} = 1.16$, $p > 0.20$). Relatively long movements occurred therefore more often, as expected by a normal distribution ($\mu \geq 3$). Further, movement lengths revealed significantly serial correlation with the previous and also the two precedent moves within all individual paths (all Spearman R, $R > 0.13$, $p < 0.01$), indicating that individuals may concentrate there foraging activity in favourable patches by repeatedly decreasing movement lengths (**Fig. 3.2**). Moreover, movement lengths were significantly correlated with absolute turning angles for 9 out of 16 individuals (all Spearman R, $R > 0.19$, $p < 0.01$). To summarize, movement trajectories from radio-tracking were characterized by the accumulation of shorter movements in some locations and occasional very long moves, indicating that these trajectories did not fit any Gaussian random walk models (Turchin 1998).

Mean turning angles (10-min intervals) were higher ($9.93 \pm 18.45^\circ$) in primary forest than in secondary forest ($2.41 \pm 20.01^\circ$). Turning angles from nightly movement paths showed

significant directional bias in 47 out of 64 (73 %) nightly paths (for all Rayleigh's $z > 0.218$, $p < 0.05$) with similar proportions among forest types (Chi²-test, $\chi^2 = 1.10$, $p = 0.29$). However, averaged nightly movement trajectories for individuals showed more variability in directional bias in secondary forest than in primary forest (CV Rayleigh's statistics, M.-W.-U test, $U_{7,9} = 12.0$, $p < 0.05$). Spatial autocorrelation in geographical positions along subsequent movement steps analysed by Mantel statistics were detected in 26 out of 64 nightly movement paths (41 %, all Mantel test $p < 0.05$), suggesting that the remaining 38 paths were relatively tortuous.

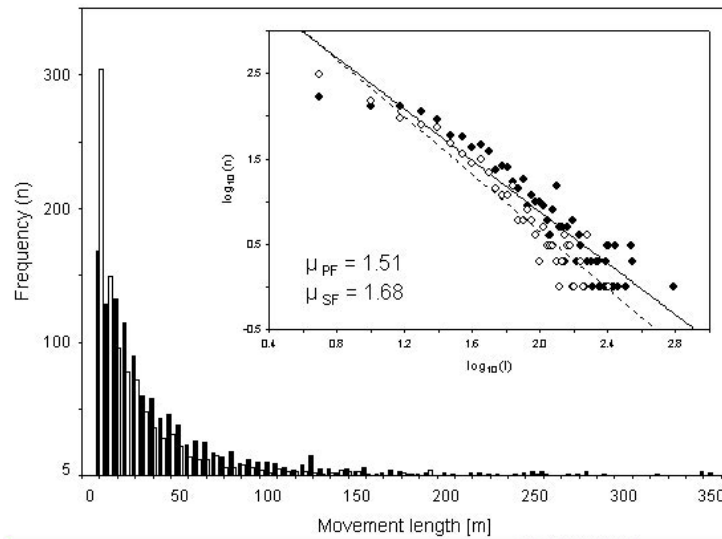


Fig. 3.4. Distribution of movement lengths from radio-tracking data during 10-min intervals for giant rats moving in primary (PF, black) and secondary forest (SF, white). The inset shows a log-log plot of the same data fitted with regression lines (both $r^2 > 0.80$) where μ is the exponent of the power law. The estimated values are nearly the same with $\mu = 1.51$ for primary forest and $\mu = 1.68$ for secondary forest (Student's t -test $t_{v=88} = -0.62$, $p > 0.50$). Frequency distributions are based on a bin size of 5 m with $n = 1,152$ movements from primary forest and $n = 989$ movements from secondary forests. Lévy flights comprise a distribution of $1 < \mu \leq 3$.

3.4.3 Activity time and ranging areas

Giant rats emerged from their burrow between 17:40 and 20:40 (mean $18:41 \pm 0:33$) with a nightly activity period averaging 485 ± 109 min. The shortest recorded activity period was for a male (SM1) in secondary forest; he was only active for about two hours (138 min) between 19:30

and 23:30. The longest activity period was that of a female (PW 7) who was active for more than 11 hours (> 680 min) between 18:20 and 5:40 in primary forest. Duration of activity periods did not differ between primary and secondary forest (M.-W.-U test, $U_{9,7} = 27.5$, $p = 0.95$) but they varied significantly among individuals (all $1.5 \leq CV \leq 21.4$, ANOVA $F_{15,48} = 7.38$, $p < 0.01$). Casual tracking at daytime confirmed that giant rats were mainly inactive during the day and remained inside their burrows, although they may occasionally be active in the vicinity of the burrow, as we found two female rats to be occasionally active during the day.

Nightly total ranges (95 % kernels) of individuals varied from 534.98 to 8986.67 m² and core ranges (50 % kernel) ranged from 92.15 to 675.76 m². Core ranges comprised on average 13.6 ± 0.4 % of the total ranges and were proportionally smaller in secondary forests than in primary forest when all nights were treated separately (M.-W.-U, $U_{36,28} = 315$, $p < 0.05$). Mean total and core ranges of individuals were marginally larger in secondary forest than in primary forest (both M.-W.-U, $13.0 \leq U_{9,7} \leq 14.0$, $0.05 \leq p \leq 0.07$) and marginally larger for males than for females (both M.-W.-U, $14.0 \leq U_{9,7} \leq 15.0$, $0.06 \leq p \leq 0.09$). Individual variation of total and core ranges among nights was high, as indicated by the high values of the coefficient of variation with a mean $CV = 29.3 \pm 19.28$ for total ranges and a $CV = 24.8 \pm 23.8$ for core ranges. Core ranges varied significantly more for individuals in secondary forest than in primary forest (CV 50 % kernel, M.-W.-U, $U_{7,9} = 12.0$, $p < 0.05$) but not for total ranges (CV 95 % kernel, M.-W.-U, $U_{7,9} = 16.0$, $p = 0.10$). The large variation in ranges within consecutive nights did not lead to significant differences of range sizes between individuals (ANOVA, $F_{15,48} < 1.16$, $p \geq 0.33$) (**Fig. 3.5**).

The various estimates of movement and ranging trajectories given above revealed some correlations (see **Table 3.3**) but in summary, large-scale movement paths were not distinct among forest types or sex as confirmed by multivariate ordination and cluster analysis (results not shown).

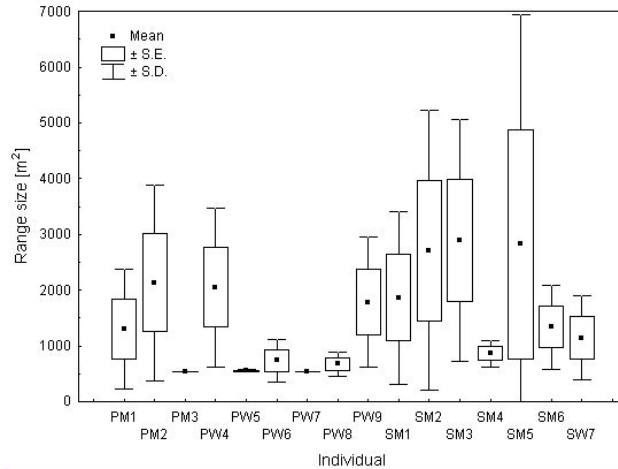


Fig. 3.5. Total range size (95 % kernel) of rats tracked for four consecutive nights in primary (PM1 – PW 9) and secondary (SM 1 – SW 7) forests. Mean total ranges varied from $535 \pm 6 \text{ m}^2$ to $2,891 \pm 2,171 \text{ m}^2$ among individuals but were not distinct because of the inherent variation (ANOVA $F_{15,48} < 1.16$, $p \geq 0.33$).

3.4.4 Use of burrows

In total, we located 27 different burrows from spool-and-line and radio-tracking. Twenty-four burrows were subterranean. Four burrows were located close to a stream and the ground inside was partially wet. The smallest entrance hole was 40 mm in diameter, whereas most entrances were between 50 - 70 mm in diameters; some burrows had at least two separate entrances. Three burrows were located in cavities of trees or logs with entrances 1 - 1.6 m above ground level. We further detected a resting site made of plant fibres formed into a pad in a cavity below a dense stand of climbing bamboo *Dinochloa spp.* in a secondary forest. In two instances, we observed an adult male sharing a burrow with an adult female. In one instance, a female was recorded sharing a burrow with a juvenile, and co-occupancy of burrows was also observed for juveniles. Up to four juveniles were recorded in the proximity of the same burrow and were likely to be siblings. A spiny rat (*Maxomys cf. surifer/rajah*) was found to enter a burrow that had been occupied previously by an immature giant rat 12 days before.

Table 3.3. Variation in movement and range trajectories from radio-tracking data. Minimum and maximum means are from individual estimates (four consecutive nights). Spearman's R correlations ($p < 0.05$) between variables from nightly estimates are given by their respective abbreviations with '-' indicating a negative correlation. Nightly CVs are means based on individual estimates to represent the variability in trajectories between nights. Total CVs were calculated from means from different individuals to represent the variability in trajectories among individuals. F-statistics from ANOVA estimate differences of variables among individuals, with significant values being marked with *.

Variable		Min. – Max. Means	Correlations	Nightly CV [%]	Total CV [%]	F from ANOVA
Nightly path length [m]	(PL)	278 – 6,328	ML, T, -Tot, - Cor, -Mr	14.0 ± 6.5	17.2	20.9*
Move length (10 min) [m]	(ML)	4.9 – 100.0	PL, -Tot, -Mr	9.4 ± 2.5	14.1	9.3*
Turning angle mean [°]	(α)	- 37.32 – 73.89	--	28.58 ± 8.72	24.2	6.8*
Activity time [min]	(T)	138 – 680	PL, Mr	7.0 ± 4.7	4.9	7.8*
Total range (95% kernel) [m ²]	(Tot)	528.7 – 8,986.7	-PL, -ML, Cor, -RR	29.3 ± 19.3	14.1	1.2
Core range (50 % kernel) [m ²]	(Cor)	92.2 – 2,604.6	-PL, Tot, -RR	24.8 ± 23.8	21.7	1.0
Raleigh's R	(RR)	0.05 – 0.89	-Tot, -Cor	27.9 ± 17.4	7.8	1.6
Mantel r	(Mr)	-0.11 – 0.49	-PL, -ML, T	45.9 ± 97.7	22.3	2.0*

3.5 DISCUSSION

Tropical rainforests represent a natural mosaic of habitat patches on multiple scales, given the large diversity of trees and other components that are heterogeneously distributed in the forest matrix (Condit *et al.* 2002). Consequently, differences in resource allocation among patches should influence movement trajectories of animals according to the size and distribution of patches relative to the movement and ranging area of animals. An important and unresolved questions is, whether different local conditions faced by moving individuals are of influence on their movement patterns. Further, it is in question whether movement patterns on larger scales

within hierarchical landscapes are simply an aggregate of movement patterns at smaller scales or subject to a different ruling mechanism (see Kotliar & Wiens 1990).

We have found qualitatively different path trajectories for giant rats on two scales, suggesting that patterns of movement comprise separate domains in which different aspects of environmental features and/or intrinsic behavioural constraints are important. Such distinct domains in movement patterns are consistent with other studies of vertebrates (Johnson *et al.* 2002; Fritz *et al.* 2003; Nams & Burgeois 2004). However, such patterns are not self-evident for our data given the finding that the small-scale tracks (total lengths of 55 ± 21 m) are within the range of distances covered within 10-min-intervals from large-scale movements (32 ± 45 m). The increasing evidence for scale-invariance from studies of movement trajectories of various vertebrates (Viswanathan *et al.* 1996; Atkinson *et al.* 2002; Ramos-Fernández *et al.* 2004) and rainforest structures (Solé & Manrubia 1995; Solé *et al.* 2005) over certain scales urges us to consider whether links between the two domains examined in our study are realistic despite their different characteristics. Such relationships are also of particular interest in the context of different path trajectories in unlogged versus logged forests, where we would expect synchronized changes across scales in a scale-invariant system. The shorter step lengths from our small-scale analysis and the shorter movement length from our large-scale analysis (although only significant for pooled data) indicate some coinciding changes in path trajectories across domains. However, contrary to our expectations, we cannot fully separate effects of logging and individual variability on the movement and ranging patterns of giant rats.

Paths from spool-and-line tracking mostly comprised directed walks that were aimed in most cases at the burrow with presumably little foraging behaviour on the way. Under this assumption, path tortuosity at this scale might be largely governed by physical features of the environment, with the number of obstructions and supports diminishing straight-line movements. The shorter step lengths in secondary forests may be therefore interpreted as a consequence of the denser and more heterogeneous undergrowth in secondary forests. This interpretation is consistent with the observation of the higher frequency with which giants rats use interlaced supports such as climbing bamboo *Dinorchloa spp.*, rattan *Calamus spp.* or vines in secondary forest, whereas movements in primary forest are characterized by longer movements on logs or the plain forest floor (**Chapter 2**). Similarly, small changes in the movement direction of the marten *Martes americana* have been attributed to the attraction or avoidance of structural features on the smallest examined scale equivalent to small-scale movement steps in our study (Nams &

Bourgeois 2004). Path tortuosity might be also interpreted as a result of the spacing of objects that serve as target or orientation points (e.g. bushes or trees) in that directed travel is performed towards objects, but not at a larger scale considering movement between many of these points (Benhamou 1990). Furthermore, tortuous paths might simply represent the most efficient way through a medium as suggested for small-scale adjustments by albatrosses *Diomedea exulans* (Fritz *et al.* 2003). It is not clear which of these scenarios would affect path trajectories of giant rats. However, the likely impact of physical structure together with the large variability in step lengths of individuals ($CV = 153$) suggest that the patchiness in local physical structure is well represented in the observed movement patterns. Such variation under local conditions is likely to lessen differences among forest types, hence explaining why logging is not a strong predictor of changes in small-scale paths despite the observed differences in step lengths.

The large-scale patterns obtained from radio-tracking presumably correspond to the scale at which foraging activity is the most important structuring force, since resource distribution is central in mammalian movement and subsequent spacing (Ostfeld 1990; Mitchell & Powell 2004). Unfortunately, little knowledge is available regarding the kinds and proportions of food items consumed by giant rats and their distribution within the heterogeneous rainforest. The large variety of patchily distributed food sources in the dipterocarp rainforest, which are consumed by most small omnivorous mammals and also giant rats (Liat 1970; Langham 1983; Emmons 2000), implies that giant rats face a variable habitat with considerable differences in resource distribution in space and time. Dipterocarp seeds, for example, comprise a seasonal key resource to rats and other vertebrates in primary forests but are replaced by small fruits in secondary forests that are produced by pioneer trees and that are of little nutritional value to vertebrates (Curran & Webb 2000; Wells & Bagchi, in press). Regardless of the specific types of ingested food, its spatial distribution should be represented in movement paths, with an increased heterogeneity and patchiness in resource allocation leading to an increased tortuosity in the paths of rats. Therefore, we expect that the patterns of nightly movements do not meet the basic assumption for a correlated random walk, which has been proposed as a null hypothesis in models including searching activity for resources in a homogeneous landscape (Kareiva & Shigesada 1983; Turchin 1998). Our observed serial correlations in movement lengths and turning angles and the variability in movement lengths do not correspond to a normal diffusion process, instead exhibiting traits that have been described as Lévy walks (Shlesinger *et al.* 1993; Viswanathan *et al.* 1996). Such principles of Lévy searches may well apply to our large-scale

movements because of the occasional larger movements observed. Occasional larger movements may increase the chance of exploring profitable distant patches and may therefore be an adaptation of searching behaviour to the presumably unpredictable and mostly sparse resource distribution in rainforest environments (see Ramos-Fernández *et al.* 2004). However, our findings in path trajectories do not fully correspond to Lévy walks because we have found that rats regularly revisit sites and return to the same burrows. Moreover, we did not determine any scale-invariance. Such discrepancies of movement traits from a single model are expected, because models only deal with selected simplified aspects of complex movements. As a generalist species, giant rats might change their searching behaviour (e.g. search for fruits versus invertebrates) or exhibit distinct search strategies among individuals (e.g. attributable to variability in resource availability among local ranges) as suggested for herbivore ungulates (Mårell *et al.* 2002; Morales *et al.* 2004) or seals (Austin *et al.* 2004). Interestingly, the various movement and ranging parameters are multilaterally correlated and exhibit a similar range of variability among individuals (Table 3.3). Although these relationships remain unclear regarding their biological meaning without more detailed knowledge enabling concrete assignments of local conditions and the aligned foraging state, differences in dietary preferences and requirements may again affect movement and ranging to the extent that resource distribution differs in space and time. We suggest that different search strategies exhibited, for example, by changing the lengths of movements and nightly paths, may apply to different resource clumping and abundance. This leads, for instance, to differences in range size and activity time. Many fruits (e.g. dipterocarps or figs) occur spatially clumped (e.g. Condit *et al.* 2002) and are exploited until they are rotten or have germinated. This distribution and phenology could lead to directed walks to known fruiting sites followed by concentrated feeding activity at the fruiting patch. Arthropod prey, in contrast, may occur either uniformly or spatially clumped, for example, at favourable sites such as streams that are frequently explored by giant rats and other small mammals (Emmons 2000; pers. obs.). In either case, searching for arthropods might require more frequent adjustments with regard to their location, because of their high mobility and unpredictable occurrence. Such differences in food availability and selection may therefore require customized search strategies with individually variable times and effort being spent in order to fulfil nutritional requirements.

According to the argumentation presented so far, variation in movement patterns at both examined scales might be largely explained by the variation in local conditions. Although our

study design has not permitted us to directly correlate individual trajectories across scales, the impact of physical structure on small-scale trajectories might be well correlated with the influence of resource availability on large-scale trajectories. For example, undergrowth density is usually diminished near large shady fruiting trees, whereas plant composition and texture near streams should be determined by hydrological circumstances (e.g. Newberry *et al.* 1999). Conversely, dense and fast-growing vegetation is most prominent in gaps, in which light-preferring and herbivorous arthropod prey may accumulate (see Davis *et al.* 2001; Hill *et al.* 2001). The coincidence of shorter step lengths from small-scale analysis with shorter movement lengths from large-scale analysis in logged forests provokes a hypothetical link between the two scales, although this remains speculative without further investigation. First, increased undergrowth densities and obstructions in secondary forest may result in more expenditure/energy being spent on the same net dispersal distance than in a homogeneous habitat. Conversely, increased undergrowth density in logged forests might favour the locomotion of rainforest dwellers by providing more supports as has been suggested for the leaping tarsier *Tarsius diana* (Merker *et al.* 2005). Second, the more tortuous path and the larger number of structural components may alter orientation and spatial memory of the small mammals (see Etienne *et al.* 1996; Deipolyi *et al.* 2001) and, hence, the ability to remember the locations of resources or other past events. Moreover, odour or visual cues from resources (e.g. ripe fruits, invertebrates) might be attenuated by denser undergrowth or altered movements in secondary forest. One possible inference is, therefore, that the efficiency of small-scale movements might affect large-scale movements either via altered effectiveness in progression towards a perceived/targeted resource patch or via decreased resource detection abilities.

To conclude, we have found that movement patterns are highly variable among individual giant rats and reflect to a large degree heterogeneity in spatiotemporal conditions. We interpret the shorter step and movement lengths in logged forest as weak indicators of logging effects, since logging does not predict the variation in other traits such as activity times or ranges, although various movement and ranging trajectories are related to each other. Strong logging effects would thus be expected to simultaneously affect various movement traits, which was not the case in our study. In particular, the lack of differences in ranges, which comprise an important determinant of conspecific interactions and population demography (Ostfeld 1990), may indicate that population demography and density are not necessarily affected by logging. Overall, these implications give the impression that the different habitat and patch properties in disturbed forest have little effect

on giant rat population demography. Such a conclusion also emerges from trapping data, which has revealed no obvious differences in individual density or population dynamics of giant rats among sites (**Chapter 1**). However, although logged forest may retain many features relevant to movement and ranging of giant rats, interactions of dispersing rats with biotic or abiotic components of the environment are not necessarily the same. For instance, the number of helminth parasites, which are known to significantly impact performance of host populations (Dobson & Hudson 1986; Altizer *et al.* 2003) and foraging behaviour (van der Wal *et al.* 2000), were lower in *L. sabanus* in logged forests but increased in another small mammal (*Tupaia longipes*) therein (**Chapter 4**). A limited indication of differences in population performances by movement patterns in primary and secondary forests has also been suggested for the civet *Viverra zibetha*, which exhibits similar activities and ranges in both forest types but which occurs in reduced abundances in logged sites (Colon 2002 and references therein).

On the one hand, it seems surprising that the effects of logging on environmental factors that might limit an individual's behaviour are not more pronounced in movement patterns. We believe that a large quantity of complexity and plasticity in movement behaviour is a response to the heterogeneity inherent to pristine rainforest environments and also to the hierarchical influence of factors that limit the fitness of a moving animal on the various scales of travelling and habitat selection (see Bowers & Dooley 1993; Rettie & Messier 2000). Such plasticity in movement and searching behaviour might not only blur any differences between logged and unlogged forest, but also might comprise an essential prerequisite for adaptation to an anthropogenically altered landscape. The increasing disturbance of rainforests requires an understanding of the way in which wildlife species are able to cope with these habitat differences. In logged rainforests, those species that are unable to cope with altered resource availability or that fail to adapt their search and dispersal strategies face a lower survival probability. Our results add to the notion that most common small mammals are able to persist in logged forests (**Chapter 1**) but also emphasize that more integrative approaches are necessary to account for altered movement patterns at different scales and their proximate-ultimate link to factors that might explain why some species are able to cope with disturbed habitats, while others are not.

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Top left to bottom right:

- *Leopoldamys sabanus* with a radio collar.
- Massive fruit fall from a dipterocarp tree during a fruiting event in Danum Valley.
- Burrow of *L. sabanus* near a stream.
- Dipterocarp seeds on forest floor during a fruiting event.
- Handling of *L. sabanus*.
- Radio-tracking with a hand-held receiver.
- Collared *L. sabanus* feeding on a fruit.
- Injection of a subcutaneous transponder.

Impact of rainforest logging on parasitic helminth assemblages in small mammals (Muridae, Tupaiidae)

4.1 ABSTRACT

Parasitic helminths (Nemathelminthes, Plathelminthes) are ubiquitous in wild animals, with host-specific life history patterns considered as major determinants of prevalence and assemblage patterns of gastrointestinal parasites. Rainforest logging results in large-scale habitat alterations that may influence habitat conditions and population performances of wildlife and consequently change the infestation patterns of local wildlife populations. We investigated pattern of helminth species diversity in two paleotropical rats, *Leopoldamys sabanus* and *Niviventer cremoriventer* (Muridae) and two tree shrews, *Tupaia tana* and *Tupaia longipes* (Tupaiidae) in primary and secondary rainforests in Borneo by examining 337 faecal samples with faecal egg count (FEC).

Nematode eggs prevailed in 95 % of all samples with up to five (mean 1.9 ± 1.1) morphotypes. Whereas members of Strongylida were most prevalent in *L. sabanus*, *T. tana* and *T. longipes*, Spirurida dominated in *N. cremoriventer*, that revealed the lowest average nematode prevalence and FEC. Cestode eggs were only found in samples from *L. sabanus* and *T. tana* with a rather low prevalence of 28 % and 6 %, respectively. Egg shedding of strongylid and cestode eggs in *L. sabanus* was positively correlated with crude arthropod consumption as determined by assessing the amount of cuticle debris in faeces. It was negatively correlated for spirurids in *T. tana*.

Following our expectation, parasitic helminth assemblages of the examined small mammals were evidently influenced by rainforest logging. Species richness of nematode morphotypes and mean number of infections per host of *T. longipes* were significantly larger in secondary forest than in primary forest. In contrast, *L. sabanus* was more heavily infected with cestodes in primary than in secondary forest and also revealed larger egg counts for strongylids and spirurids in primary forest.

Our results suggest that forest degradation and altered environmental conditions influence helminth diversity and infestation patterns of small mammals with inconsistent pattern among host species. Approaches aimed at explaining the influence of host characters on parasite diversity should consider the way in which these factors are shaped by environmental conditions. Given that rainforest degradation could influence parasite infestation patterns in mammalian species, further analysis of parasite assemblages may serve as a valuable tool in analyzing population performances in altered habitats.

4.2 INTRODUCTION

The bottom-up or top-down processes that regulate species occurrence and consequently community composition are central themes in our understanding of mechanisms that maintain biodiversity in multifaceted trophic cascades (Brown *et al.* 2001; Terborgh *et al.* 2001; Turchin & Hanski 2001). Such interactions can be very complex for organisms in highly diverse ecosystems such as in the speciose small mammal communities in tropical rainforests and their associated gastro-intestinal nematode fauna. A better understanding of the links between parasite assemblages and the environmental setting is particularly important as parasitism is increasingly emphasised as a major biotic impact on population performance and maintenance of biodiversity (Dobson & Hudson 1986; Altizer, Harvell & Friedle 2003; Guernier *et al.* 2004). Anthropogenic habitat disturbance may profoundly change community diversity as well as species performances and interactions on various levels of trophic cascades (Terborgh *et al.* 2001), including host-parasite systems (Gillespie *et al.* 2005). On one hand, environmental stress may increase host susceptibility to diseases via reduced maintenance of the costly immune defence, whereas on the other hand, altered habitat conditions or host densities may reduce parasite transmission and establishment (e.g. Altizer, Harvell & Friedle 2003; Lafferty & Holt 2003).

In primeval rainforests, non-volant small mammals comprise diverse assemblages with various degrees of phylogenetic or ecological similarities among species that promote the successful exploitation of the entire three-dimensional habitat (Bourliere 1989; Malcolm 1995; Wells *et al.* 2004). Therefore, their parasites encounter a diverse habitat with considerable variability in habitat traits (host-specific characters) and dynamics (host mobility and space utilisation) that are likely to be important determinants for the richness of parasite species (e.g. Holt *et al.* 2003).

Conversely, parasitic nematodes have been recognised as important factors influencing host life-history strategies and population demography of their hosts (Dobson & Hudson 1986; Gulland 1995). In this mutual context, parasite speciation and establishment in particular hosts are explained both by parasite traits and by specific features of the host such as body size, diet or habitat use. One way to understand these interactions is to compare interspecific variation among host species that serve as distinct habitats (Morand 2000; Arneberg 2002; Nunn *et al.* 2003; Poulin 2004). Biological features of the host that are considered to shape helminth communities differ in their plasticity from invariable (e.g. host phylogeny, body size) to relatively variable (e.g. host diet, ranging behaviour) and, accordingly, in their plasticity in shaping associated parasite assemblages via environmental variability. However, few attempts have been made to investigate the impact of environmental changes on parasitic worm assemblages incorporating dynamic changes of relevant host features either within or between different habitat types.

Although most information on parasites and the influence of environmental variation on small mammal distribution and demography has been derived from temperate ecosystems, small mammal communities in tropical rainforests are particularly rewarding for such studies as they are highly diverse and offer dynamic habitats for associated parasites. The large diversity of patchily and sparsely distributed trees and other plants in tropical habitats (e.g. Condit *et al.* 2000) provide complex and heterogeneous forest matrices in space and time with major effects of this naturally inherent environmental variability on small mammal distribution and diversity (August 1983). The resulting temporally and spatially variable availability of resources determines species occurrences and demography, although population-level responses to structural variability may differ among species that exhibit different degrees of specialisation, including generalist species (Seamon & Adler 1996; Adler 2000). The omnivorous feeding habits of generalist and common small mammal species promote an overlap in diet and space use (Adler 2000; Emmons 2000; Wells *et al.* 2004). These potential overlaps between host species may serve as an important underlying mechanism for structuring parasitic helminth assemblages, as patterns of host sharing and host switching are subject to the specialisation and segregation of hosts in habitat use and diet. Furthermore, generalist hosts that occupy a more variable and complex habitat are exposed to a wider array of parasites than specialist hosts with a more scattered distribution (Nunn *et al.* 2003). Environmental variability may further control the encounter of host species with invertebrates that may serve as intermediate hosts.

Whereas the environmental variability inherent in undisturbed rainforests might well be part of established host-parasite dynamics, the extent to which logging, that reinforces naturally occurring variability to prominent large-scale disturbances, affects parasites from small mammals remains largely unexplored.

Many commercially logged rainforests differ drastically in floral composition and structure (e.g. Uuttera *et al.* 2000; DeWalt *et al.* 2003). Currently, the most rapid deforestation and biodiversity loss occurs in the dipterocarp rainforests of SE Asia (Sodhi *et al.* 2004). Small mammal assemblages have been found to decline in species richness in logged forests (e.g. Malcolm & Ray 2000; Lambert *et al.* 2005), although information on causes and consequences for biotic interactions remain tenuous. Even less attention has been paid to the species richness of parasitic helminth communities harboured in tropical wildlife assemblages.

Despite such shortcomings of basic information of host species and the associated helminth fauna, rapid habitat destruction and degradation and the possible consequences for disease spread impel us to improve our understanding of the affect of these changes on wild host populations and parasites (Altizer, Harvell & Friedle 2003; Ostfeld & Holt 2004). On one hand, undisturbed rainforests act as ultimate controls for naturally balanced host-parasite ensembles. On the other hand, due to rapidly progressing changes in land use, small mammal populations and associated parasites are exposed to various types of habitat disturbance that may increase environmental stress for hosts (e.g. parasite resistance) or parasites (e.g. transmission) and consequently, may alter risks and benefits of habitat disturbance from both perspectives.

In Bornean small mammal assemblages, habitat specialists and rare species are particularly susceptible to anthropogenic impacts (**Chapter 1**), predicting that future forest landscapes will be dominated by widespread generalist species. Knowledge of the way in which logging affects these species is in its infancy.

The aim of this study, therefore, has been to determine whether human-caused alterations of the rainforest environment play a role in generating patterns of parasitic helminth diversity in various small mammals. We have investigated whether changes in helminth faecal egg counts (FEC) differ between four species of murids and tupaiids and among forest types in Bornean rainforests, since changes in FEC are a suitable manifestation of the occurrence and diversity of faecally dispersed helminth parasites (Moss *et al.* 1990; Skorpung *et al.* 1991; Seivwright *et al.* 2004) and allow large sampling with little impact on animals. These helminths comprise a valuable model, since both nematodes with direct transmission (e.g. most members of the orders Strongylida,

Oxyurida) and indirect life cycles that require arthropods or other invertebrates as intermediate hosts (e.g. most Spirurida, Enoplida) (Anderson 2000) among indirectly transmitted acanthocephals (Nemathelminthes, Acanthocephala), segmented cestodes and trematodes (both Plathelminthes, Neodermata) are included. Murids and tupaiids comprise important elements of small mammal assemblages in SE Asian rainforests. These assemblages differ in their biological history, such as geographical distribution, digestive system and social interaction. All investigated species were common both in primary and secondary forest site with an increased abundance of the arboreal rat *Niviventer cremoriventer* and the terrestrial tree shrew *Tupaia tana* in secondary forest (**Chapter 1**). We addressed the question whether prevalence and richness of parasitic helminths differ in the investigated small mammal species and discussed whether possible differences in specific helminth assemblages are explainable by host traits and the crude arthropod consumption. We further hypothesized that similarities and differences in gastrointestinal helminth assemblages between primary and secondary forest are predicted by differences in host species performances in logged forest or taxonomic similarities among hosts.

4.3 METHODS AND MATERIALS

4.3.1 Study site and sampling

Small mammals were captured on Borneo (Sabah, Malaysia) in three old-growth forest sites (Kinabalu National Park 06° 02.248' N, 116° 42.482' E, Tawau Hills National Park 04°23.974' N, 117°53.436' E, Danum Valley Conservation Area 04° 57.800' N, 117° 48.173' E) and three secondary forests (Kg. Monggis 06°13.198' N, 116°45.802' E, Kg. Tumbalang 06° 08.427' N, 116° 53.912' E, Luasong Field Centre 4° 36.432' N, 117° 23.391' E). Study sites were located at distances between 17 - 236 km and comprised large forest stands of 1,000 hectares and considerably more. 100 – 130 locally made wire- mesh cage traps baited with banana were placed in three localities within each study site. Faecal samples were collected during a total of 16 sampling periods between September 2002 and June 2004. We analysed faeces from four small mammal species that were common in both primary and secondary forests (**Table 4.1**).

Faeces from first captures or recaptures of animals that were individually marked with AEG transponders were collected from the floor below the trapped animals and stored in 3 % formalin. Faeces were collected in the morning after a trapping night and animals were released once their

sex, age, weight and biometric measurements including head-body (HF), tail (T) and length of hind feet (HF) had been determined. Animals were aged and classified as juvenile, immature, subadult or adult based on pelage and development of external sex organs.

Table 4.1. Morphological and ecological characteristics of study species.

Species	Family	Weight [g]	HB [mm]	Habitat
Long-tailed giant rat <i>Leopoldamys sabanus</i>	Muridae	368 ± 64 (n = 101)	292 ± 13 (n = 84)	terrestrial, occasionally arboreal
Long-tailed tree rat <i>Niviventer cremoriventer</i>	Muridae	69 ± 13 (n = 142)	125 ± 8 (n = 144)	terrestrial, arboreal
Large tree shrew <i>Tupaia tana</i>	Tupaiaidae	218 ± 27 (n = 126)	189 ± 7 (n = 110)	terrestrial, scansorial
Common tree shrew <i>Tupaia longipes</i>	Tupaiaidae	196 ± 25 (n = 59)	191 ± 8 (n = 51)	terrestrial, scansorial

4.3.2 Faecal egg count protocol

We counted all eggs from nematodes (Nemathelminthes) as well as cestodes and trematodes (Plathelminthes) based on faecal samples with a modified flotation and McMaster method (Thienpont *et al.* 1986; Meyer-Lucht & Sommer 2005). This non-invasive technique has been shown to be accurate for quantification of helminth eggs (e.g. Moss *et al.* 1990; Skorping *et al.* 1991; Seivwright *et al.* 2004). We used potassium iodide solution (specific gravity 1.5 g/ml) for egg flotation. Samples of approximately 600 mg faeces (mean 570 ± 92 g) were dissolved in 9 ml solution, sieved to remove large debris and screened for helminth eggs by counting the content of two chambers of a McMaster slide. All eggs were photographed and measured (Zeiss, AxioCam and AxioVision software; 10 – 40 × amplification). Images were then assigned to operational taxonomical units (orders for nematodes, cestodes) based on features of egg shell and plasma and further distinguished by size classes and shell thickness (for strongylids), if applicable. We simultaneously counted the number of non-transparent arthropod fragments down to sizes between 10 - 200 µm on the McMaster slides to assess the proportion of arthropod consumption of the hosts. We noted the number of cuticles per gram (CPG) of faeces to obtain a faecal cuticle count (FCC).

4.3.3 Statistical analysis

We considered all egg morphotypes that could be identified as helminth eggs for analysis of overall infestation patterns. However, we took only egg classes that could be identified to orders for estimates of diversity and null model analysis of co-occurrence patterns. Infection status of individuals was indicated by the number of helminth morphotypes found in each individual and, for each morphotype, by the number of eggs per gram of faeces (EPG). Faecal samples from recaptures (14 out of 337) were considered for analysis with more than six months between captures. The counts of eggs and number of cuticles per gram were log-transformed for analysis with $FEC = \log_{10} (EPG + 1)$ and $FCC = \log_{10} (CPG + 1)$, respectively. Samples were pooled for each host species among sites ($n = 3$) for analysis of differences in infestation rates and parasite diversity between primary and secondary forests. FEC were calculated separately for all eggs assigned to different orders and only nematode eggs, respectively.

In order to measure randomness in co-occurrence patterns of identified nematode orders, we used a null model analysis based on the average number of checkerboard units ('C-score', calculated from the number of shared orders in data matrix) (see Haukisalmi & Henttonen 1998; Gotelli & Rohde 2002). Observed patterns on the co-occurrence of identified nematode orders were compared with 5,000 randomly assembled combinations by applying the EcoSim 7.0 software (Gotelli & Entsminger 2004, <http://garyentsminger.com/ecosim/index.htm>). Although we were only able to distinguish eggs by orders and size classes, thereby leaving some eggs unclassified (194 out of 710 classifications), we assumed that the number of recorded morphotypes increased with the true species number in samples and therefore that diversity calculations based on presence-absence data of all classified eggs were accurate for comparative approaches. Diversity estimates were calculated with EstimateS 7.5 (Colwell 2005, <http://purl.oclc.org/estimates>).

As diversity estimates are strongly dependent on sample size and coverage (Magurran 2004), sample orders were randomised 50 times and all comparisons were made on standardised minimum sample sizes. Chao2 species richness estimator was chosen based on sample coverage (Brose *et al.* 2003). Nematode community diversity was determined using Simpson's (reciprocal) index D (see Magurran 2004). We used non-parametric statistics for all comparisons among variables, as we merely intended to confirm that one variable was higher than another, rather than considering the extent of the divergence. Means are given as ± 1 S.D. and the significance of post hoc pair-wise comparisons was tested with Dunn's test.

4.4 RESULTS

4.4.1 Helminth diversity and interspecific host patterns

We screened a total of 337 faecal samples from four species of small mammals: 158 samples from *L. sabanus* (with seven samples from individuals recaptured in a consecutive trapping session), 23 samples from *N. cremoriventer* (23 ind.), 125 samples from *T. tana* (118 ind.), and 31 samples from *T. longipes* (31 ind.). We found nematodes of the orders Strongylida, Spirurida, Enoplida, and Oxyurida and cestodes. We found no acanthocephalan eggs and no trematode infestation, although a single egg in a sample from *T. tana* might have been a trematode.

Combining all species of small mammals, nematode eggs were prevalent in 319 out of 337 samples (95 %) with zero to five (mean 1.9 ± 1.1) morphotypes per host individual. Nematode eggs of the orders Strongylida (1-6 size classes per host species) and Spirurida (1-5 size classes) were prevalent in both, rat and tree shrews, whereas Oxyurida were found only in rat samples (*L. sabanus*, *N. cremoriventer*); Enoplida (1-2 size classes) was not found in *N. cremoriventer* (Table 4.2).

Table 4.2. Prevalence (% infected) of nematode orders and cestodes in the different host species. The numbers of faecal samples are given in parenthesis.

Helminth	Prevalence [%]			
	<i>L. sabanus</i> (n = 158)	<i>N. cremoriventer</i> (n = 23)	<i>T. tana</i> (n = 125)	<i>T. longipes</i> (n = 31)
Strongylida	74.1	30.4	75.2	90.3
Spirurida	34.8	56.5	35.2	19.4
Oxyurida	4.4	8.7	0	0
Enoplida	8.9	0	4.0	6.5
Cestoda	27.8	0	6.4	0
Total prevalence (%)	94.9	82.6	96.8	96.8
Number of nematode morphotypes	1.9 ± 1.1	2.1 ± 1.3	1.8 ± 1.0	1.2 ± 0.7

Strongylids were most prevalent in *L. sabanus*, *T. tana* and *T. longipes*, and spirurids dominated in *N. cremoriventer* (Fig. 4.1). The number of nematode infections was significantly correlated with FEC of nematode eggs for all host species (all Spearman $R > 0.316$, $p < 0.01$). The mean

number of nematode infections and egg counts was significantly different between host species (Kruskal-Wallis-ANOVA $H_{3,337} = 12.941$, $p < 0.01$) with the lowest prevalence of nematodes in *N. cremoriventer* (Fig. 4.2).

Null model analysis of co-occurrence patterns of the different nematode morphotypes did not differ from a random distribution for any host species (all $p > 0.11$).

Cestodes occurred less frequently than nematodes. They were only found in 44 out of 158 samples (28 %) from *L. sabanus* and eight out of 125 samples (6 %) from *T. tana* with zero to two (mean 0.17 ± 0.41) infestations per individual.

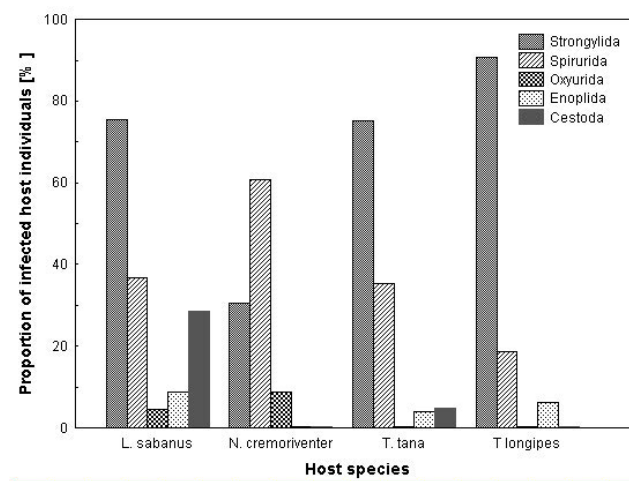


Fig. 4.1. Proportion of host individuals infected with nematodes and cestodes.

L. sabanus $n = 158$, *N. cremoriventer* $n = 23$, *T. tana* $n = 125$, *T. longipes* $n = 31$.

4.4.2 Influence of host characteristics on infestations

The number of nematode morphotypes was not related to host sex, age, weight or biometric measurements (HB, T, HF) for the four host species (sex: all M.-W.-U tests $p > 0.44$, age: all Kruskal-Wallis ANOVA $p > 0.29$, biometric measures: all Spearman R correlations $p > 0.19$). However, FEC measures differed significantly between age classes for *L. sabanus* and *N. cremoriventer* with an increased count for adults (both Kruskal-Wallis ANOVA $H > 9.2$, $p < 0.05$). Although overall nematode egg count increased significantly with weight, HB and T for *N. cremoriventer* (all Spearman $R_{n > 21} = 0.45$, $p < 0.05$), FEC was significantly correlated with HF size for *T. tana* (Spearman $R_{n = 106} = 0.19$, $p < 0.05$). The abundance of cestode eggs increased among age classes of *L. sabanus* (Kruskal-Wallis ANOVA $H_{3,154} = 8.10$, $p < 0.05$).

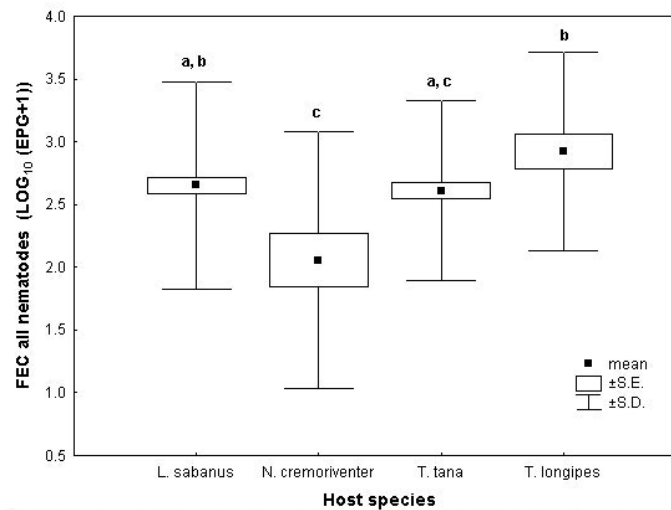


Fig. 4.2. Mean FEC of all nematodes from the different host species (Kruskal-Wallis-ANOVA $H_{3,337} = 12.941$, $p < 0.01$). Boxes with different letters above indicate significant differences (Dunn's test).

4.4.3 Crude arthropod consumption and egg counts

The crude arthropod consumption as estimated by FCC was neither correlated to the number of nematode morphotypes nor to the entire nematode FEC for the four host species. However, strongylid egg counts were significantly correlated with the FCC for *L. sabanus* (Spearman $R_n = 117 = 0.26$, $p < 0.01$) with fewer cuticle fragments being counted for uninfected or only lightly infected (EPG 1-500) individuals compared with medium (EPG 501-1,500) infected individuals (**Fig. 4.3**). Further, FCC were greater for *L. sabanus* infected with cestodes than for non-infected individuals (M.-W.-U, $U_{85,32} = 1,024.5$, $p < 0.05$). Egg counts of spirurids decreased with increasing FCC for *T. tana* (Spearman $R_n = 125 = -0.29$, $p < 0.01$), for which FCC were larger for non-infected individuals (M.-W.-U, $U_{81,44} = 1,110$, $p < 0.01$).

4.4.4 Parasitic load of small mammals in primary versus secondary forests

Randomised species accumulation curves revealed that species richness of parasites, based on morphotypes of nematodes, was not apparently different between primary and secondary forest for *L. sabanus* (**Fig. 4.4a**). Different morphotypes were more quickly accumulated in primary forest than in secondary forest for *T. tana* (**Fig. 4.4b**). However, despite this indication of higher nematode species richness in primary forest, samples size was not sufficient for a reliable

estimate of species richness. In contrast, nematode species richness estimated from accumulation curves was significantly higher in secondary forest than in primary forest for *T. longipes* (**Fig. 4.4c**).

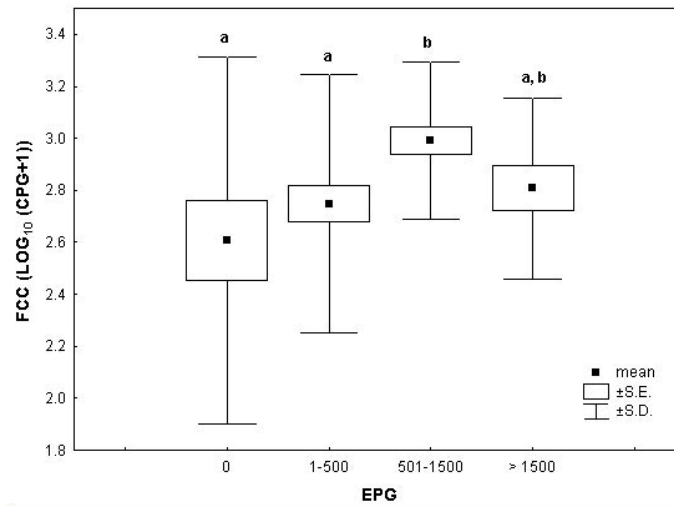


Fig. 4.3. Mean cuticle counts (FCC) of samples from *L. sabanus* in relation to relative abundance of strongylid eggs (EPG, Kruskal-Wallis-ANOVA $H_{3,117} = 9.29$, $p < 0.05$). Boxes with different letters above indicate significant differences.

This was also confirmed by the Chao2 estimates, which were 3.99 ± 0.29 for primary forest and 8.34 ± 2.34 for secondary forest for nematodes eggs recovered from *T. longipes*. Diversity patterns differed for all three species between primary and secondary forest (**Table 4.3**) when combining species richness and heterogeneity with the Simpson's index. The mean number of nematode infections per host individual was significantly larger for *T. longipes* in secondary than in primary forest (M.-W.-U, $U_{19,12} = 39.5$, $p < 0.01$). Egg counts for strongylids and spirurids were significantly larger in primary than in secondary for *L. sabanus* (both M.-W.-U $U_{98,60} > 2,066$, $p < 0.05$).

Cestodes were significantly more prevalent in *L. sabanus* in primary than in secondary forest (M.-W.-U, $U_{98,60} = 2,005$, $p < 0.01$); 19 % of all individuals were infected in primary forest compared with 7 % in secondary forest. Counts of cestode eggs were also larger in primary forest (M.-W.-U, $U_{98,60} = 1,875$, $p < 0.01$).

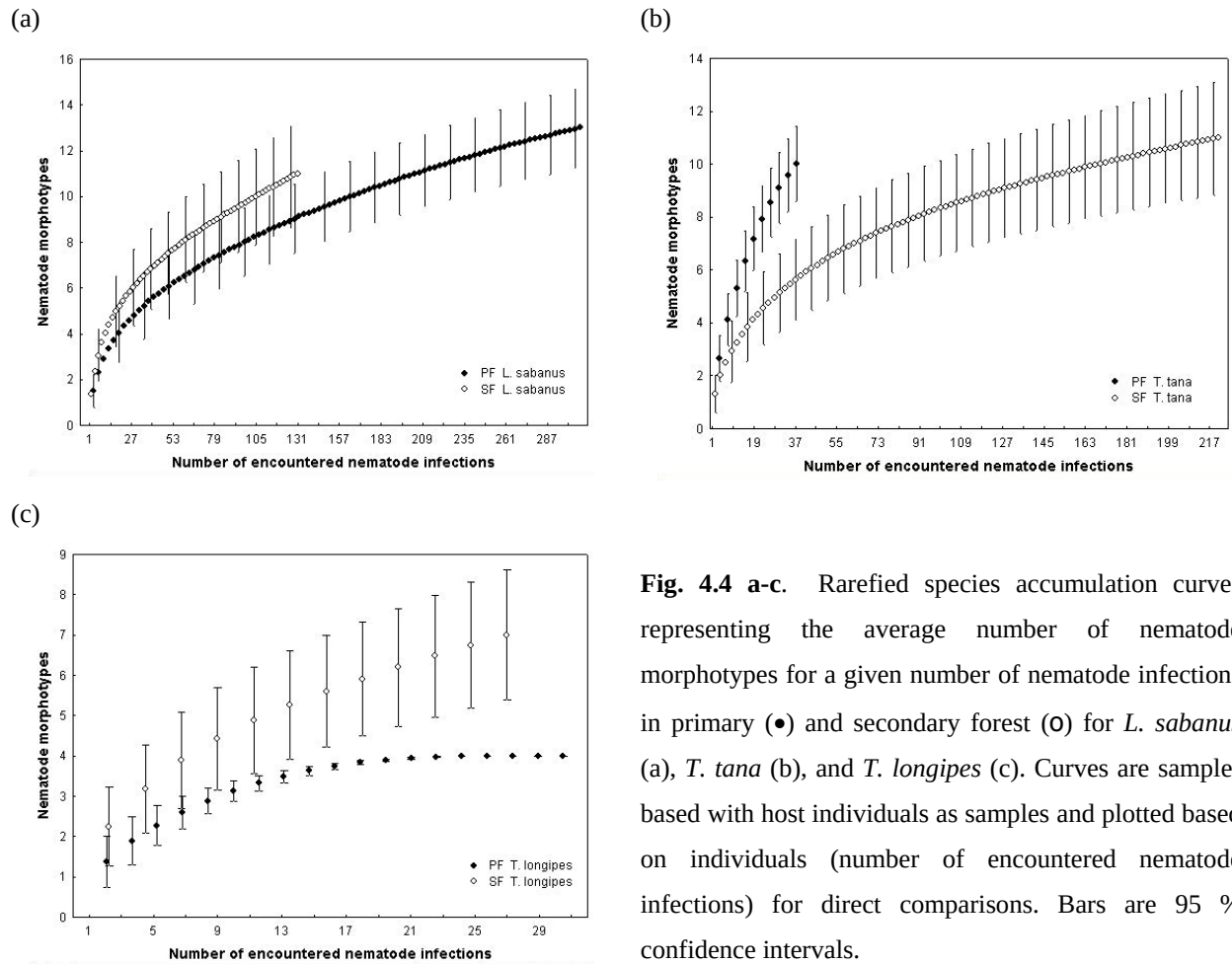


Fig. 4.4 a-c. Rarefied species accumulation curves representing the average number of nematode morphotypes for a given number of nematode infections in primary (●) and secondary forest (○) for *L. sabanus* (a), *T. tana* (b), and *T. longipes* (c). Curves are sample-based with host individuals as samples and plotted based on individuals (number of encountered nematode infections) for direct comparisons. Bars are 95 % confidence intervals.

Table 4.3. Chao2 species richness estimate and Simpson's D diversity indices based on nematode morphotypes found in hosts captured in primary (PF) and secondary (SF) forest. Calculations are based on a randomised order of the minimum standardised number of samples per forest type (given in parenthesis). *N. cremoriventer* is excluded from the analysis because of insufficient sample size.

Species		<u>Chao2</u>		<u>Simpson's D</u>	
		PF	SF	PF	SF
<i>L. sabanus</i>	(n = 60)	16.5 ± 5.8	20.8 ± 10.0	3.51 ± 0.51	2.7 ± 0.3
<i>T. tana</i>	(n = 30)	11.5 ± 2.1	9.1 ± 2.6	3.58 ± 0	2.7 ± 0.42
<i>T. longipes</i>	(n = 12)	4.0 ± 0.3	8.4 ± 2.3	2.7 ± 0.59	4.03 ± 0.15

4.5 DISCUSSION

Mammalian species comprise well-defined habitats for parasites with respect to a range of important characters such as body size, diet and spacing pattern, although the variability inherent in heterogeneous rainforest matrices presumably provides variable conditions for parasites via inconsistent patch and resource exploitation of some host species. Habitat variability and disturbance of rainforests, which is pronounced on a large scale in logged forest, have been associated with altered gastrointestinal parasites assemblages from African primates in logged forests (Gillespie *et al.* 2005). The present study recorded first data on distinct helminth assemblages in tropical murids and tupaiids that were evidently affected by rainforest logging.

The results of our study show that the helminth assemblages differed quantitatively and qualitatively in the distribution of nematodes and cestodes among hosts. Given the conservative estimate from FEC and the rough scale classification of morphotypes, neither the tracing of definite species nor the calculation of absolute species richness has been possible. However, our data are valuable for comparative approaches and the question as to why particular orders of nematodes are favoured in certain hosts. Differences in helminth assemblages among hosts were most apparent in the arboreal rat *N. cremoriventer*, where the nematode fauna is dominated by spirurids rather than strongylids as in the other three host species and the lowest numbers and intensities (FEC) of infections were recorded. Conversely, the composition of helminth assemblages was most similar for *L. sabanus* and *T. tana*, with similar prevalences of strongylids and spirurids and cestodes present in both species (see Fig. 4.2). Among host clades, the only resemblance we found was the distribution of oxyurids, which have been recorded in rats but not in tree shrews. The absence of certain parasite groups must be treated with some caution, especially for *N. cremoriventer* and *T. longipes*, as helminth species are likely to escape detection, whereas prevalences might be overestimated with relatively small samples sizes (Poulin 1998).

Observed similarities in helminth assemblages are worth considering in the context of habit overlap of host species, which might increase interspecific transmission of helminths via interspecific contact, use of contaminated substrate, or foraging on the same intermediate hosts. For instance, directly transmitted nematodes should be more widespread if other host individuals forage within a contaminated habitat patch in which defecation has taken place (Vander Wal *et al.* 2000; Ezenwa 2003). Generally, ubiquitous small mammals probably overlap with other species, increasing the probability for associated parasites by host sharing (generalist parasites) or

shifting (specialist parasites). Indeed, microhabitat and resource utilisation seems to overlap considerably for generalist species on the rainforest floor (Emmons 2000; Wells *et al.* 2004). Habitat utilisation has been found to be similar for the terrestrial/scansorial active *T. tana* and *T. longipes* (**Chapter 2**), and habitat overlap between *T. tana* and *L. sabanus* (terrestrial and occasionally arboreal) is likely, as both species have some affiliation to wet habitats and live close to streams (Emmons 2000; K. Wells, pers. obs.). This overlap in space use may therefore contribute to the high prevalence of strongylids in *L. sabanus* and both tree shrews. In contrast, *N. cremoriventer* is the only species examined that frequently approaches the canopy and possibly spends a considerable proportion of time there.

Presumably, this variation in host habitat use also provides divergent conditions for transmission and development across parasites (see Anderson 2000). Arboreal life is associated with many changes in biotic and abiotic factors, including invertebrate abundance and the foraging and feeding habits of mammals (Emmons 1995). Presumably, the arboreal activity of *N. cremoriventer* and other arboreal species might preclude the establishment of directly transmitted strongylids, as the dropping of faeces during arboreal activity may reduce contamination of the foraging habitat, although not necessarily for larger host species such as primates (Freeland 1980). Further, arboreal activity reduces exposure to the soil stages of some nematodes. This may explain the lower prevalence of strongylids compared with arthropod-transmitted spirurids in *N. cremoriventer*. Scarcity or absence of certain vectors along habitat gradients such as arboreal versus terrestrial, together with host feeding preferences, might also explain the lack or low prevalence of indirectly transmitted helminths. Furthermore, the intensive and rapid relocation of faeces, particularly from the tropical forest floor, by dung beetles (Scarabaeidae) and ants (Formicinae) may influence the spread of faecally transmitted eggs (e.g. directly transmitted strongylids), as has been discussed for seed removal from piles (e.g. McConkey 2005; Vander Wall *et al.* 2005). Such complex dynamics may, on the one hand, reduce transmission and, on the other, promote vertical transfer among hosts by translocating eggs among different microhabitat patches. Such a scenario may help to explain why directly transmitted helminths, such as strongylids and oxyurids, are not necessarily the most prevalent in tropical small mammals, such as the arboreal *N. cremoriventer*. The extent of arboreal activity may contribute to the pattern of helminth prevalence and richness observed but, with only one truly arboreal species having been examined, whether the relatively low parasite density recorded in *N. cremoriventer* is solely related to arboreal life remains ambiguous. Some nematodes, such as trichostrongylids or the

trichurid *Capillaria*, seem to share hosts that include both terrestrial and arboreal murids (Liat *et al.* 1977; Hasegawa & Syafruddin 1997). Although some information on specific helminth assemblages from the Indomalayan region are available (Ow Yang 1971; Liat 1970; Liat *et al.* 1975; Ow Yang *et al.* 1983), our rough estimate does not allow any insights into whether host sharing is a common phenomenon that may also blur differences between host species at the level of helminth orders.

Diet and nutritional status influence host interaction with parasites as well. The spectrum of invertebrates eaten by a host determines the exposure to intermediate hosts and the encounter probability of parasites with indirect life cycles. Such relationship may for example account for the lack of trematode infections in the examined species, which require snails as intermediate hosts or herbage infected with viable cercaria/ metacercaria to be part of the regular host diet. In particular, the extremely variable food resources of the examined small mammals suggest that feeding on invertebrates varies with environmental conditions and resource availability. The observed relationships between crude arthropod intake and FEC have revealed no consistent patterns among host and parasite species. Whereas FEC of strongylids and the number of cestode infections in *L. sabanus* were positively correlated to crude arthropod intake, spirurid egg counts and the number of infection are negatively related to arthropod debris in *T. tana*. In theory, a correlation between spirurid or cestodes eggs and arthropod debris should be more likely as ingested arthropods may serve as intermediate hosts, whereas this background can not account for a relationship between strongylid and arthropod debris as found for *L. sabanus*. We suggest that such relationship may be due to a higher abundance of arthropods in places where the area is contaminated by parasite eggs as the rats forage.

Increased faecal egg counts have been also related to low levels of protein intake in mice (Slater & Keymer 1986) and in artiodactyls (Ezenwa 2004), supporting the idea that host nutrition status can be related to immune depression and resistance against parasite establishment (Coop & Holmes 1996). In addition, low protein level may enhance feeding motivation and, consequently, parasite encounter by feeding preferably on arthropods (indirectly transmitted helminths) or extending foraging in space or time (monoxenous parasites). Resource and nutrient availability in disturbed rainforests differ from undisturbed rainforests because of changes in plant (e.g. Uuttera *et al.* 2000; DeWalt *et al.* 2003) and invertebrate (e.g. Davis *et al.* 2001; Floren & Linsenmair 2001; Cleary 2005) communities. Changes in nutritional conditions in logged forests have been suggested to increase gastrointestinal parasite prevalence and richness in an African frugivorous

primate, whereas those from folivorous primates were not affected (Gillespie *et al.* 2005). Although our data do neither reveal any consistent relationship between arthropod debris and worm burdens nor do we have detailed information on nutritional status of host species, the finding that nutrition and helminth infection are related in this host-parasite system adds another point that may be of relevance for changes in helminth assemblages in logged rainforests. We found logging to cause various changes in helminth infections among the hosts that we cannot interpret consistently with known host traits. Helminth assemblages in *L. sabanus* and *T. tana* were less diverse in logged forest, concurrent with reduced species richness and lower egg counts of strongylids, spirurids and cestodes in *L. sabanus* in logged sites. Conversely, diversity and species richness of helminths were higher in *T. longipes* in secondary forest, resulting in larger numbers of infections per host individual in disturbed forest. As pointed out above, host characters, such as diet, abundance, range and interspecific contact influence parasitism (Altizer *et al.* 2003; Nunn *et al.* 2003) and these factors might well be affected by logging. The impact of logging on species demography has been found to be weak for *L. sabanus*, *T. tana* and *T. longipes*, with only *T. tana* increasing slightly in its abundance in logged forests (**Chapter 1**). Hence, the pattern of helminth parasitism in logged forests can not solely be explained by changes in host densities, spacing patterns, or taxonomy.

Fluctuations of host abundance and interspecific contact are predicted to have most impact on directly transmitted parasites, whereas the variation in intermediate host abundances among definitive hosts may lead to variation in parasite species richness that is independent of the characteristics of host species (Morand & Poulin 1998; Arneberg 2002). Therefore, the effects of forest degradation may differ among directly and indirectly transmitted parasites. Unfortunately, we do not have detailed information on the invertebrates ingested by the host nor on the effects of logging on potential intermediate hosts. On the one hand, assuming that some intermediate host species are not tolerant towards logging because of altered arthropod communities in logged forest (references above), parasites with indirect life cycles should have a lower chance of encountering optimal conditions in an altered habitat and of following the colonisation of new habitat patches by their hosts. On the other hand, logging leads to greater canopy openness and respective changes in abiotic factors. Normally, the rainforest ground is moist and cool in contrast to the canopy and, thus, the extensively modified microclimate in logged sites (partially resembling upper strata conditions) may also influence hypobiosis (arrested development) and the conditions for free-living stages of directly transmitted parasites (see Anderson 2000).

In conclusion, parasite establishment in any particular host seems to be controlled by a set of multiple factors that vary at the environmental, host, and parasite level. Even within single functional or taxonomic groups, little evidence has been collected to date for uniform effects of rainforest logging on species richness and performances (Hamer & Hill 2000). The concept of multidirectional outcomes for diverse species interactions seems to be applicable to our study, which demonstrates altered but contrasting patterns of parasitism for various small mammal species in logged forests.

Considering the central role that parasites play in host ecology and performances (Dobson & Hudson 1986; Altizer, Harvell & Friedle 2003), ongoing habitat and landscape alterations make it crucial to elucidate the influence on environmental changes on host-parasite relations in free-ranging wildlife and possible outcomes for wildlife diversity. Our data demonstrate that parasitic helminth assemblages are affected by logging in murids and tupaiids from Bornean rainforests. Helminth assemblages revealed considerable dissimilarities among host species, and the effects of logging on these parasites were unpredictable between hosts. Without further detailed information on the impact and changes of host ecology, resource availability and parasite systematics and transmission pattern, it is not possible to precisely determine proximate mechanisms that are responsible for these consequences. Nevertheless, the inconsistent logging-induced changes in helminth assemblages from different hosts suggest that specific sets of habitat-host-parasite interactions are uniquely determined by the effects of logging. Further research is needed to investigate whether general patterns in altered parasite assemblages emerge if a larger quantity of host species is being examined and to test whether host population performances in altered habitats are linked to associated parasites and vice versa. Changes in parasite assemblages reported here are examined for logging treatment only, but particularly the multifaceted factors that we suggested to contribute to these patterns anticipate that different types of structural (e.g. type and extent of logging) or areal (e.g. fragmentation and edge sizes) habitat disturbances may lead to different outcomes. Investigating further changes in parasite assemblages provides a promising perspective to understand the various outcomes of different types of anthropogenic habitat disturbances on wildlife and whether environmental stress in altered habitat is increasing host infestation via reduced host immune defence or diminishes parasitism via adverse condition for parasite transmission. These information may help in predicting small mammal dynamics and subsequent small mammal-induced ecosystem changes in logged forest that enable more informed assessment and decision making for managing habitat

disturbance. In addition, possible multiple host systems in wildlife parasites promote disease emergence from wildlife (Cleaveland *et al.* 2001) and, thus, the identification of the host status of sympatric wildlife species is essential in disease management. Further research on parasite infections in wildlife together with risk and benefit considerations of habitat destruction and degradation are therefore of importance from both conservation and public health perspectives.

4.6 REFERENCES

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Top left to bottom right:

- Village in the forest of the Crocker Range.
- Arable land of a villager adjacent to forest.
- An emergent *Koompasia* tree.
- Plank sawing for private house construction.
- Selective tree harvest for private use.
- Traditional small mammal traps.
- Oil palm refinery.
- Oil palm plantation.
- Forest edge in Danum Valley.

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Curriculum Vitae

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2002 - present	University of Ulm, Germany	Ph.D. candidate in animal and tropical ecology.

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1995 – 1996	Community service and research assistance on migrating birds Institute of Avian Research „Vogelwarte Helgoland“, Heligoland, Germany
2002	Technical research assistance Department of Experimental Ecology, University Ulm, Germany
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2000	Project work “Arboreal ants as key predators in tropical lowland rainforest trees”, Kinabalu Park, Sabah, Malaysia
2001	Fieldwork M.Sc. thesis “Diversity, dynamics and spacing patterns of a small mammal community in a primary rainforest in Sabah, Malaysia”, Kinabalu Park, Sabah, Malaysia
2002-2004	Fieldwork Ph.D. project “Impact of rainforest logging on non-volant small mammal assemblages in Borneo”, Sabah, Malaysia
2004-2005	Guest scientist “Universiti Malaysia Sabah”, Sabah, Malaysia

Refereed Publications

- Wells, K., Pfeiffer, M., Lakim, M.B. & Linsenmair, K.E. (2004) Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia. *Journal of Biogeography*, **31**, 641-652.
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Erklärung

Hiermit erkläre ich, die vorliegende Dissertationsarbeit selbständig angefertigt und keine anderen als die in der Arbeit aufgeführten Hilfsmittel verwendet zu haben. Wörtlich oder inhaltlich übernommene Stellen wurden als solche gekennzeichnet.

Ulm, den 03. November 2005