Journal of Tropical Ecology (2007) **23**:35–43. Copyright © 2007 Cambridge University Press
doi:10.1017/S0266467406003804 Printed in the United Kingdom

Impact of rain-forest logging on helminth assemblages in small mammals (Muridae, Tupaiidae) from Borneo

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(*Accepted 16 October 2006*)

Abstract: Parasites are ubiquitous in wild animals, with host-specific life histories considered as major determinants of prevalence and parasite assemblage patterns. It is predicted that habitat differences in logged rain forests influence population performances of small mammals and consequently may change the infection patterns of local animal populations with regard to endo- and ectoparasites. We investigated patterns of helminth species assemblages (Nematoda, Platyhelminthes) in two rat species (*Leopoldamys sabanus*, *Niviventer cremoriventer*) and two tree shrew species (*Tupaia tana*, *T. longipes*) in three logged and three unlogged rain forests in Borneo by examining 337 faecal samples with non-invasive 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 at the same time the lowest average nematode prevalence and FEC. Cestode eggs were only found in *L. sabanus* and *T. tana*. Composition and abundance patterns of the parasitic helminth assemblages were influenced by logging. As hypothesized, species richness of nematode morphotypes and mean number of infections per host of *T. longipes* were larger in logged than in unlogged forest. In contrast, *L. sabanus* was more heavily infected with cestodes in unlogged than in logged forest and also revealed larger egg counts for strongylids and spirurids in unlogged forest. Our results suggest that forest degradation and altered environmental conditions influence helminth diversity and infection patterns of small mammals with contrasting trends among host species. The inconsistent logging-induced changes in helminth assemblages from different hosts indicate that specific sets of habitat-host-parasite interactions are uniquely influenced by the effects of logging. Consequently, predictions on changes of parasite diversity and prevalence with regard to habitat disturbance need to be based on the individual life histories of the hosts (and the parasites).

Key Words: Host-parasite interactions, infection risk, helminths, parasite diversity, logging, small mammals

INTRODUCTION

The bottom-up or top-down processes that regulate species occurrence and 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). Such interactions can be very complex for organisms in highly diverse ecosystems such as the species-rich communities of small mammals in tropical rain forests and their associated ecto- and endo-parasites. Habitat disturbance profoundly affects and changes 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). Environmental stress may increase host susceptibility to diseases via reduced maintenance of the costly immune defence, whereas altered habitat conditions or host densities may reduce parasite transmission and establishment (Altizer *et al.* 2003, Lafferty & Holt 2003, Ostfeld & Holt 2004).

In tropical rain forests, non-volant small mammals comprise diverse assemblages, which exploit the entire three-dimensional space (Malcolm 1995, Wells *et al.* 2004). Their parasites encounter a diverse habitat with considerable variability in habitat traits (host-specific characters) and dynamics (host mobility and space

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utilization). Parasite speciation and establishment in particular hosts are explained both by parasite traits and by specific characteristics of the host ranging from invariable (e.g. host phylogeny, body size) to variable (e.g. diet, ranging behaviour) features. The high diversity, large number and patchy distribution of tree species and other plants in tropical forests provide complex and heterogeneous forest matrices in space and time (Condit *et al.* 2000). In this context, population-level responses of small mammals to variability in structure and resource availability are likely to differ among species that exhibit different degrees of specialization (Seamon & Adler 1996). The omnivorous feeding habits of generalist and common small-mammal species, for example, promote an overlap in diet and space use (Adler 2000, Emmons 2000, Wells *et al.* 2004). These potential overlaps between host species may be central for structuring parasite assemblages, as patterns of host sharing and host switching are subject to the 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).

The extent to which logging-induced disturbances affect parasites from small mammals remains largely unexplored. Many commercially logged rain forests differ drastically in structure and floristic composition from undisturbed forests (DeWalt *et al.* 2003). Small-mammal assemblages have been found to decline in species richness in logged forests (Lambert *et al.* 2005, Malcolm & Ray 2000, Wells, unpubl. data), although detailed information on causes and consequences for biotic interactions is largely lacking.

Due to rapidly progressing changes in land use in South-East Asia (Sodhi *et al.* 2004), small-mammal populations and associated parasites are exposed to various types of habitat disturbance that increase environmental stress for hosts (e.g. parasite resistance) or parasites (e.g. transmission) and consequently, alter risks and benefits of habitat disturbance from both perspectives.

Murids and tupaiids comprise important elements of small-mammal assemblages in South-East Asian rain forests. These assemblages differ in their biological history, such as geographical distribution, digestive system and social interaction. The aim of this study has been to determine whether human-caused alterations of the rain-forest environment play a role in generating patterns of parasitic helminth diversity in various small mammals. We thus hypothesized that differences in gastro-intestinal helminth assemblages between logged and unlogged forest are determined by taxonomic similarities among hosts and interspecific differences in host species performances in logged forest.

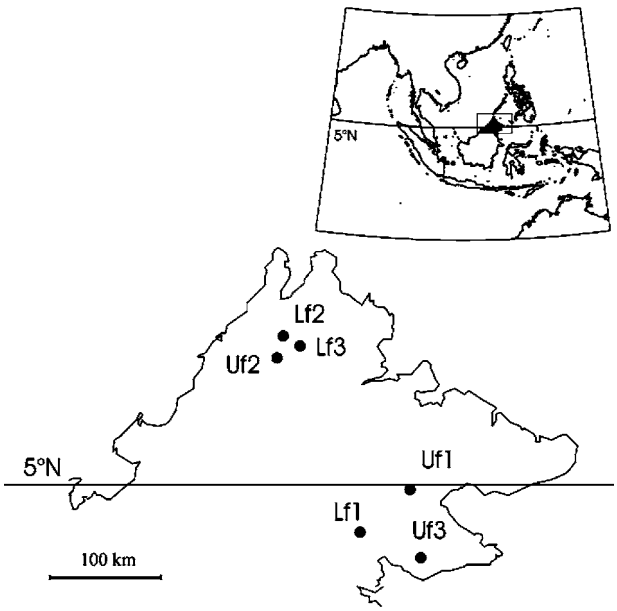

Figure 1. Map of northern Borneo with the six study sites. Unlogged forests: Danum Valley Conservation Area 'Uf1'; Kinabalu NP 'Uf2'; Tawau Hills NP 'Uf3'; logged forests: Luasong Field Centre 'Lf1'; Kg. Monggis 'Lf2'; Kg. Tumbalang 'Lf3'.

METHODS

Study site and sampling

Small mammals were captured on Borneo (Sabah, Malaysia) in three old-growth forest sites (Kinabalu National Park, 06°02′N, 116°42′E; Tawau Hills National Park, 04°23′N 117°53′E; Danum Valley Conservation Area, 04°57′N 117°48′E) and three logged forests (Kampong Monggis, 06°13′N, 116°45′E; Kampong Tumbalang, 06°08′N, 116°53′E; Luasong Field Centre, 04°36′N 117°23′E) (Figure 1). Study sites were located at distances between 17–236 km; all of the forest stands comprised at least 1000 ha. We placed 100–130 wire-mesh cage traps baited with banana in three localities within each study site and conducted a total of 16 sampling periods of 16 d each, continuously alternating between the different forest sites between September 2002 and June 2004. Faeces were collected in the morning after a trapping night. Animals were released once their sex, age (juvenile, subadults, adults; based on pelage and reproductive organs), weight and biometric measurements including head-body (HB), tail (T) and length of hind feet (HF) had been determined. First captures of individuals were permanently marked with transponders (ARE 162, AEG) and faeces were collected from the floor below the trapped animals and stored in 3% formalin. We analysed faeces from four common small-mammal species (Muridae, Tupaiidae; Table 1) that occurred in logged and in unlogged forests.

https://doi.org/10.1017/S0266467406003804 Published online by Cambridge University Press

Table 1. Morphological and ecological characteristics of study species.

Species	Family	Weight (g)	Head–body length (mm)	Habitat
Leopoldamys sabanus	Muridae	368 ± 64 (n = 101)	292 ± 13 (n = 84)	Terrestrial, occasionally arboreal
Niviventer cremoriventer	Muridae	69 ± 13 (n = 142)	125 ± 8 (n = 144)	Terrestrial and arboreal
Tupaia tana	Tupaiidae	218 ± 27 (n = 126)	189 ± 7 (n = 110)	Terrestrial, scansorial
Tupaia longipes	Tupaiidae	196 ± 25 (n = 59)	191 ± 8 (n = 51)	Terrestrial, scansorial

Faecal egg count protocol

We counted all eggs from nematodes (Nematoda) as well as cestodes and trematodes (Platyhelminthes) from the faecal samples with a modified flotation and McMaster method (Meyer-Lucht & Sommer 2005). This non-invasive technique has been shown to be accurate for estimating the number of helminth eggs. However, egg counts do not fully correspond to adult worm burden (Moss *et al.* 1990, Seivwright *et al.* 2004, Skorping *et al.* 1991). We used potassium iodide solution (specific gravity 1.5 g ml^{-1}) for egg flotation. Samples of approximately 600 mg faeces (mean ± SD = 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 eggshell and content and further distinguished by size classes and shell thickness for strongylids. We simultaneously counted the number of non-transparent arthropod fragments down to 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).

Data analysis

We considered all egg morphotypes that could be identified as helminth eggs for analysis of overall infection patterns. However, we took only egg classes that could be identified to order 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) in consecutive sampling periods with more than 6 mo between captures were considered for analysis. 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). Samples were pooled for each host species among sites (n = 3) for analysis of differences in infection and parasite diversity between logged and unlogged forests. FEC were calculated separately for all eggs assigned to different orders and only nematode eggs, respectively.

Although we were only able to distinguish eggs by orders and size classes (194 out of 710 unclassified), we assume that the number of recorded morphotypes increases 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 (http://purl.oclc.org/estimates).

As diversity estimates are strongly dependent on sample size and coverage, sample orders were randomized 50 times and all comparisons were made on standardized 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 (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. Mean ± 1 SD is given and the significance of post hoc pair-wise comparisons was tested with Dunn's test.

RESULTS

Helminth diversity and interspecific host patterns

We screened a total of 337 faecal samples from four species of small mammal: 158 samples from *Leopoldamys sabanus* (with seven samples from individuals recaptured in a consecutive trapping session), 23 samples from *Niviventer cremoriventer* (23 individuals), 125 samples from *Tupaia tana* (118 individuals), and 31 samples from *T. longipes* (31 individuals). We found nematodes of the orders Strongylida, Spirurida, Enoplida and Oxyurida as well as cestodes. We found no acanthocephalan eggs and no trematode infection, although a single egg in a sample from *T. tana* might have been a trematode. As trematode eggs, unlike eggs from other helminths, are too heavy to reliably float up in potassium iodide solution, a few eggs may have been missed.

Combining samples from all species of small mammal, nematode eggs were prevalent in 319 out of 337

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Table 2. Prevalence (per cent infected) of nematode orders and cestodes in the different host species. The numbers of faecal samples are given in parentheses.

	Prevalence (%)			
Helminth	*Leopoldamys sabanaus* (n = 158)	*Niviventer cremoriventer* (n = 23)	*Tupaia tana* (*n* = 125)	*Tupaia longipes* (*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
Mean number of nematode morphotypes	1.9 ± 1.1	2.1 ± 1.3	1.8 ± 1.0	1.2 ± 0.7

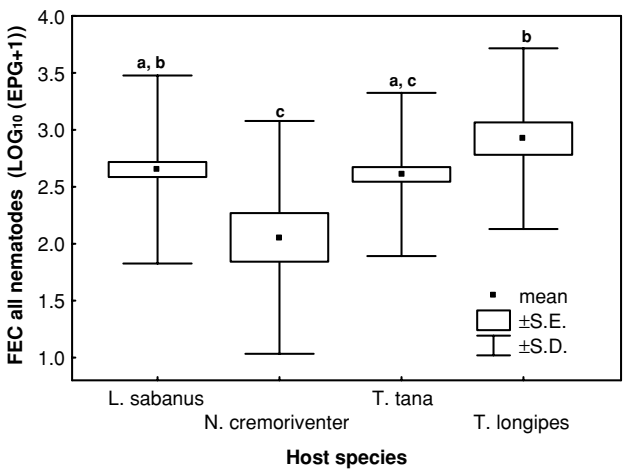

Figure 2. Mean faecal egg count (FEC) of all nematodes from the host species *Leopoldamys sabanus*, *Niviventer cremoriventer*, *Tupaia tana* and *T. longipes* (Kruskal–Wallis ANOVA $H_{3,337} = 12.9$, $P < 0.01$). Different letters above whiskers indicate significant differences (Dunn's test).

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) were not found in *N. cremoriventer* (Table 2). Strongylids were most prevalent in *L. sabanus*, *T. tana* and *T. longipes*, whereas spirurids dominated in *N. cremoriventer*. 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 differed significantly between host species (Kruskal–Wallis ANOVA $H_{3,337} = 12.9$, $P < 0.01$; Figure 2) with the lowest prevalence of nematodes in *N. cremoriventer* (Table 2). Cestodes occurred less frequently than nematodes and 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. 2 ± 0.4) infections per individual.

Influence of host characteristics on infections

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 Mann–Whitney U-tests $P > 0.44$, age: all Kruskal–Wallis ANOVA $P > 0.29$, biometric measures: all Spearman 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 $H > 9.2$, $P < 0.05$). Overall nematode egg count increased significantly with host weight, HB and T in *N. cremoriventer* (all Spearman $R_{n>21} = 0.45$, $P < 0.05$), while 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 $H_{3,154} = 8.10$, $P < 0.05$).

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 $R_{n=117} = 0.26$, $P < 0.01$) where fewer cuticle fragments had been found in uninfected or only lightly infected (EPG 1–500) individuals compared with medium (EPG 501–1500) infected individuals (Figure 3). Further, FCC were higher for *L. sabanus* infected with cestodes than for non-infected individuals ($U_{85,32} = 1024$, $P < 0.05$). 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 ($U_{81,44} = 1110$, $P < 0.01$).

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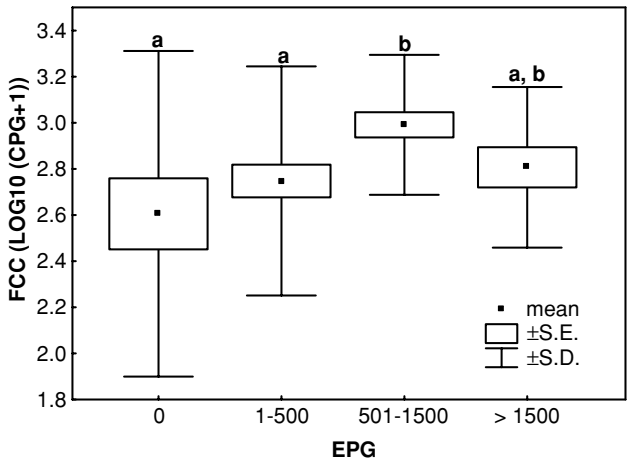

Figure 3. Mean cuticle counts (FCC) of samples from *Leopoldamys sabanus* in relation to relative abundance of strongylid eggs (EPG, Kruskal–Wallis ANOVA $H_{3,117} = 9.29$, $P < 0.05$). Different letters above whiskers indicate significant differences (Dunn's test).

Parasitic load of small mammals in logged versus unlogged forests

Randomized species accumulation curves revealed that species richness of parasites, based on morphotypes of nematodes did not differ between logged and unlogged forest for *L. sabanus* (Figure 4a). In contrast, nematode species richness estimated from accumulation curves was significantly higher in logged forest than in unlogged forest for *T. longipes* (Figure 4b). This was also confirmed by the Chao2 estimates, which were 8.3 ± 2.3 for logged forest and 4 ± 0.3 for unlogged forest for nematode eggs recovered from *T. longipes*. Different morphotypes accumulated faster in samples from unlogged forest than for logged forest for *T. tana* (Figure 4c). However, samples size was not sufficient for a reliable estimate of species richness in this host species.

Diversity patterns differed in all small-mammal species studied between logged and unlogged forest (Table 3)

Table 3. Chao2 species richness estimate and Simpson's D diversity indices based on nematode morphotypes found in hosts captured in unlogged (UF) and logged (LF) forest. Calculations are based on a randomized order of the minimum standardized number of samples per forest type (given in parentheses). *Niviventer cremoriventer* is excluded from this analysis because of small sample size

	Chao2		Simpson's D	
Species	UF	LF	UF	LF
Leopoldamys sabanus (n = 60)	16.5 ± 5.8	20.8 ± 10.0	3.51 ± 0.51	2.7 ± 0.3
Tupaia tana (n = 30)	11.5 ± 2.1	9.1 ± 2.6	3.58 ± 0	2.7 ± 0.42
Tupaia longipes (n = 12)	4.0 ± 0.3	8.4 ± 2.3	2.7 ± 0.59	4.03 ± 0.15

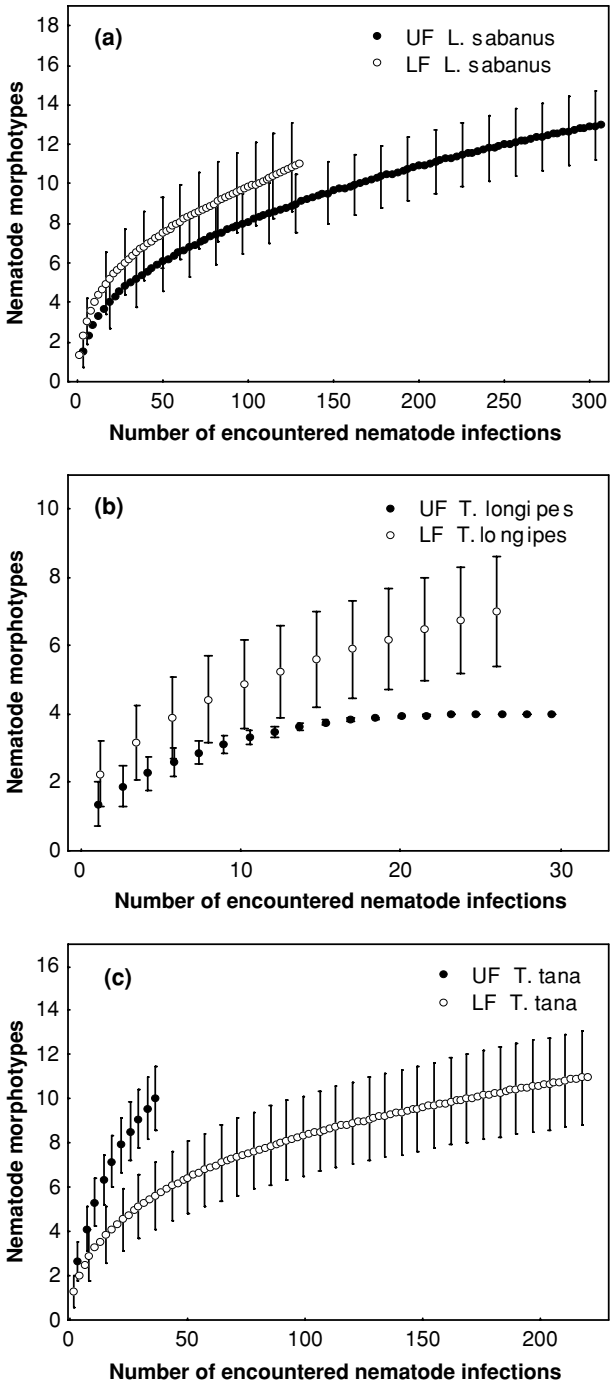

Figure 4. Rarefied species accumulation curves representing the average number of nematode morphotypes for a given number of nematode infections in unlogged (●) and logged forest (○) for *Leopoldamys sabanus* (a), *Tupaia longipes* (b) and *T. tana* (c). Curves are sample-based with host individuals as samples and plotted based on individuals (number of encountered nematode infections) for direct comparisons. Bars are 95% confidence intervals.

when combining species richness and heterogeneity with the Simpson's index. The mean number of nematode infections per host individual was significantly larger for

https://doi.org/10.1017/S0266467406003804 Published online by Cambridge University Press

T. longipes in logged than in unlogged forest ($U_{19,12} = 39.5$, $P < 0.01$). Egg counts for strongylids and spirurids were significantly larger in unlogged than in logged forest for *L. sabanus* (both $U_{98,60} > 2066$, $P < 0.05$).

Cestodes were significantly more prevalent in *L. sabanus* in unlogged than in logged forest ($U_{98,60} = 2005$, $P < 0.01$); 19% of all individuals were infected in unlogged forest compared with 7% in logged forest. Counts of cestode eggs were also higher in unlogged forest ($U_{98,60} = 1875$, $P < 0.01$).

Overall, helminth assemblages did not show any apparent differences within or between logged versus unlogged forests in *L. sabanus* or *T. tana* in terms of overlap in helminth morphotypes (Sørensen similarity index; both $U_{6,9} > 25.5$, $P > 0.19$). We found two strongylid morphotypes in the faeces of *T. tana* in logged forests and none in unlogged forest.

DISCUSSION

Mammalian species comprise well-defined habitats for parasites with respect to a range of important characters such as body size, diet, mobility and spacing pattern. An important factor that is likely to add a high degree of variability into the system is the heterogeneity of rain-forest matrices that is likely to be associated with variable conditions for parasites via inconsistent patch and resource exploitation of host species. The present study assessed first data on distinct helminth assemblages in tropical small mammals, in particular murids and tupaiids, which were affected by rain-forest logging.

Interspecific differences in helminth assemblages among hosts were most apparent in the arboreal rat *Niviventer cremoriventer*, in which the nematode fauna was dominated by spirurids rather than strongylids as in the other three host species and where we recorded the lowest numbers and intensities (FEC) of infections. Conversely, the composition of helminth assemblages was most similar in *Leopoldamys sabanus* and *Tupaia tana*: both revealed similar prevalences of strongylids, spirurids and cestodes. Among host clades, the distribution of oxyurids was the only difference. They were recorded in rats but not in tree shrews. However, the absence of certain parasite groups must be treated with some caution, especially for *N. cremoriventer* and *T. longipes*, as helminth species are difficult to detect. Further, prevalences might be overestimated when sample size is relatively small (Poulin 1998).

Observed similarities in helminth assemblages need to be seen in the context of habitat overlap of host species, which might increase interspecific transmission of helminths via interspecific contact, use of contaminated substrate, or feeding on the same intermediate hosts. For instance, directly transmitted nematodes are likely to be more widespread if other host individuals forage within a contaminated habitat patch in which defecation has taken place (Ezenwa 2003, Vander Wal *et al.* 2000). Generally, ubiquitous small mammals overlap in habitat use with a number of other mammal species, increasing the probability for associated parasites by host sharing (generalist parasites) or shifting (specialist parasites). In particular, use of similar habitats has been found for the terrestrial/scansorial tree shrews *T. tana* and *T. longipes* (Wells *et al.* 2006). Further, habitat overlap is also likely between *T. tana* and *L. sabanus* (terrestrial and occasionally arboreal), as both species are affiliated to wet habitats and streams (Emmons 2000, K. Wells pers. obs.). In contrast, *N. cremoriventer* is the only species in this study that frequently forages in the canopy.

Presumably, variation in host habitat use, i.e. terrestrial and arboreal, provides divergent conditions for transmission and development across parasites (see Anderson 2000) because of the differences in abiotic and biotic factors encountered in the respective habitats (Emmons 1995). The arboreal activity of *N. cremoriventer* and other species might preclude the establishment of directly transmitted strongylids, as faeces is dropped during activity in the trees, thus reducing contamination of the occupied habitat. Further, arboreal activity reduces exposure of the hosts to the soil stages of some nematodes. This may explain the lower prevalence of strongylids compared with arthropod-transmitted spirurids in *N. cremoriventer*. Furthermore, the rapid relocation of faeces by dung beetles (Scarabaeidae) and ants (Formicinae) may also influence the spread of faecally transmitted eggs (e.g. directly transmitted strongylids), as has been discussed for seed removal from piles (McConkey 2005, Vander Wall *et al.* 2005).

While such complex dynamics may, on the one hand, reduce transmission, they may, on the other, promote vertical transfer among hosts by translocating eggs among different microhabitats. This may help to explain why directly transmitted helminths did not necessarily dominate. We are also aware that the result of relatively low parasite density recorded in the arboreal *N. cremoriventer* is solely based on one example. Moreover, some nematodes, such as trichostrongylids or the trichurid *Capillaria*, appear to share hosts that include both terrestrial and arboreal murids (Hasegawa & Syafruddin 1997, Lim *et al.* 1977).

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. In particular, the high variability in food use of the examined small mammals suggests that feeding on invertebrates strongly varies with environmental conditions and resource availability. The observed relationships between crude arthropod intake and FEC did

not reveal consistent patterns among host and parasite species. FEC of strongylids and the number of cestode infections in *L. sabanus* were positively correlated with crude arthropod intake, whereas spirurid egg counts and the number of infections were negatively related to arthropod debris in *T. tana*. Theoretically, a correlation between spirurid or cestodes eggs and arthropod debris should be more likely as ingested arthropods may serve as intermediate hosts, whereas this relationship does not account for strongylids and arthropod debris as found in *L. sabanus*. Probably, a higher abundance of arthropods fosters such a relationship in places where the area is contaminated by parasite eggs. In addition, low protein level of an animal may enhance feeding motivation and, consequently, parasite encounter by feeding preferably on arthropods (indirectly transmitted helminths) or extending foraging in space or time (monoxenous helminths).

Resource and nutrient availability in logged rain forests differ from undisturbed rain forests because of changes in plant (DeWalt *et al.* 2003) and invertebrate communities (Cleary *et al.* 2005, Davis *et al.* 2001, Floren & Linsenmair 2001). For instance, changes in nutritional conditions in logged forests have been suggested to increase gastrointestinal parasite prevalence and richness in an African frugivorous primate in contrast to folivorous primates that were not affected (Gillespie *et al.* 2005). Although our data do not reveal any consistent relationship between arthropod debris and worm burdens, nor do we have detailed information on nutritional status of host species, our finding that nutrition and helminth infection are related in this host–parasite system adds another important point to the question how changes in helminth assemblages are influenced by rain-forest logging.

Interestingly, some of the observed differences in helminth infections between logged and unlogged forest cannot be interpreted consistently with known host traits. While helminth assemblages in *L. sabanus* and *T. tana* were less diverse in logged forest, diversity, species richness and the prevalence of helminths were higher in *T. longipes* in logged forest. This contrasts with the impact of logging on species demography which has been found to be rather weak for these generalist species (Wells, unpubl. data). Hence, the pattern of helminth parasitism in logged forests cannot solely be explained by changes in host densities, spacing patterns or taxonomy.

Overall, fluctuations in host abundance and interspecific contact are predicted to have most impact on directly transmitted parasites. Conversely, variation in the abundance of vectors associated with the various definitive hosts may lead to variation in parasite species richness that is independent of the characteristics of host species (Arneberg 2002, Morand & Poulin 1998). Hence, 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 hosts nor on the effects of logging on potential intermediate hosts. Assuming that some intermediate host species do not tolerate logging because of alterations in arthropod communities, parasites with indirect life cycles should have a lower chance of encountering optimal conditions in an altered habitat and of following the colonization of disturbed habitat patches by their hosts. On the other hand, logging leads to greater canopy openness and respective changes in abiotic factors. Typically, rain-forest understoreys are moist and cool in contrast to the canopy. Extensive modifications caused by logging lead to changes in microclimate at the logged sites. Drier and hotter conditions may influence the conditions for free-living stages of directly transmitted parasites, for instance, by fostering hypobiosis (arrested development) (Anderson 2000).

Parasite establishment in any particular host is controlled by a set of factors that vary at the environmental, host and parasite level. Because of the multitude of factors, it is difficult to predict the outcome of particular changes in the system as each component may be affected differently. Our study confirms this notion as it demonstrated multidirectional outcomes of logging on parasite assemblages in small mammals. On one hand, parasite assemblages of small mammals were altered in composition and relative abundance of selected taxa in response to logging. On the other hand, however, our study also revealed contrasting patterns of parasitism which means that factors act differently on the individual components of the system.

Further research is needed to investigate whether more general patterns in altered parasite assemblages emerge if a larger quantity of host species is examined. Investigating changes in parasite assemblages provides a promising perspective to understand the various outcomes of different types of anthropogenic habitat disturbances on mammals and whether environmental stress in altered habitat is increasing host infection via reduced host immune defence or diminishes parasitism via adverse conditions for parasite transmission.

ACKNOWLEDGEMENTS

Many thanks are due to Maklarin B. Lakim, Sabah Parks, Malaysia, for his support and amicable collaboration during fieldwork. Sabah Parks, Yayasan Sabah, the Royal Society SE-Asia Rainforest Research Programme (SEARR), and the University Malaysia Sabah granted access to forest sites and are thanked for all kinds of support. The Economic Planning Unit Malaysia kindly issued a research permit. We are further indebted to Jörg Ganzhorn and Simone Sommer for providing laboratory facilities and hospitality at Hamburg University. Yvonne

Meyer-Lucht kindly shared her experience on faecal egg analysis. Many people in Sabah, among them Alim Biun, Awang Matamin, Jikson Sankin, Lajimi Mail and Suati Selimon, provided valuable help in the field. Thanks are due to anonymous referees for constructive comments on earlier drafts. The German Academic Exchange Service (DAAD) kindly provided financial support.

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