NEST SITES OF RODENTS AND TREESHREWS IN BORNEO

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Abstract. We used spool-and-line and radio-tracking to discover 83 nests of seven non-volant small mammal species in the tropical rainforest of Borneo. Terrestrial rats of the genus *Maxomys* (*M. rajah* and *M. surifer*), and the occasionally arboreal rat *Leopoldamys sabanus*, used mostly subterranean burrows, whereas the arboreal rat *Niviventer cremoriventer* utilized above-ground nests of plant fiber or leaves fixed on various branches. The scansorial squirrel *Sundasciurus lowii* nested both in tree cavities and in nests made of plant fiber. Treeshrews (*Tupaia tana* and *T. longipes*) used both subterranean and above-ground nesting sites. Nesting patterns were thus distinct among species, but revealed no apparent association between any nest type and features of the surrounding habitat such as vegetation density. Above-ground nests made of plant fibers were of similar size and construction for *S. lowii* and *T. tana*, and an individual of *M. rajah* was seen entering a burrow that had been previously occupied by *L. sabanus*, indicating that there is likely some interspecific overlap in nest sites. *Accepted 29 June 2006.*

Key words: *Muridae, nesting behavior, tree cavities, tropical rainforest, Tupaiidae.*

INTRODUCTION

As one makes one's bed, so must one lie in it, and nearly all species of small mammals require nests as denning sites, shelter, sleeping sites, or places to raise offspring (we use the term 'nest' for all types of nests/ shelters/refuges because we were not able to distinguish between these uses). The architectural characteristics and location of nests are of key importance in many aspects of a small mammal's life. Nests must provide protection from predators and adverse climate (Kolbe & Janzen 2002). When resting or raising offspring, mammals may have altered metabolism and be less alert to counteract ambient influences. The available space inside a nest determines the number of individuals that can aggregate, and nest size might be chosen based on the inhabitants' social organization. Further, nest conditions can influence parasite prevalence and transmission, which in turn might determine host distribution patterns and frequency of nest switching (e.g., Roper *et al.* 2002, Krasnov *et al.* 2003). For species that depend on pre-existing structures such as tree cavities, distribution and population density may be limited by the availability of such cavities or woody debris. Human-caused forest changes, such as logging of tropical rainforests, may further re-

duce the availability of tree cavities and woody debris (e.g., Laurance 1990, Ganzhorn & Schmid 1998, DeWalt *et al.* 2003). Features of nest sites, including nest concealment, architecture, and accessibility to various predators, may affect the inhabitant differently under different habitat conditions. (e.g., Cooper & Francis 1998). Therefore, type and location of nest sites are likely to affect survival and reproductive success and may also play a role in structuring small mammal communities.

It can prove difficult to locate the nest sites of cryptic and little-known small mammals in rainforests, and, for most species, habitat types used for nesting and architecture of nests are unknown. However, spool-and-line tracking has improved our ability to locate nests (e.g., Miles *et al.* 1981, Boonstra & Craine 1986, Briani *et al.* 2001).

Furthermore, in Borneo, nests of treeshrews have been located and described by radio-tracking of various species (Emmons 2000), revealing distinctive nesting patterns among species. Conversely, the burrows of rodents, which are the most common species in terrestrial and arboreal small mammal assemblages on Borneo and elsewhere in the tropics (Bernard 2004; Wells *et al.* 2004a), have not yet been described.

Here we report on nest sites of seven common small mammal species from the families Muridae, Sciuridae, and Tupaiidae in a Bornean rainforest, for
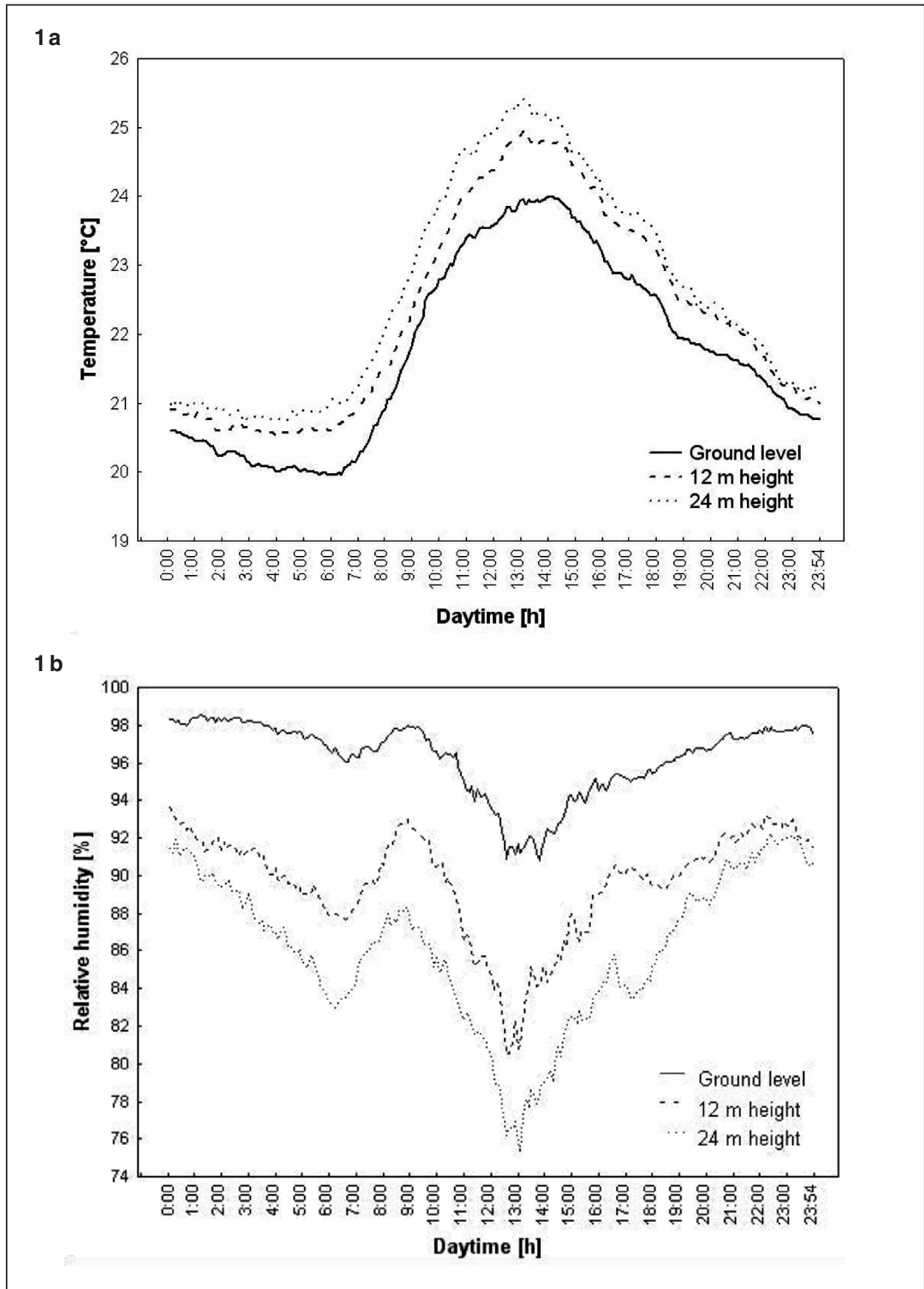
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1a

1b

FIG. 1 a, b. Daily temperature (a) and humidity (b) curves at three different heights, averaged over 15 days between March and September 2001 in the unlogged forest of Kinabalu Park.

which we tracked individuals while pursuing aspects of small mammal movement and habitat utilization in logged and unlogged rainforests (Wells *et al.* 2006).

METHODS AND MATERIALS

The tropical lowland forests on the island of Borneo harbor more vascular plant species than any other ecoregion on earth (Kier *et al.* 2005), including 3000 species of trees (MacKinnon *et al.* 1996). In this structurally complex habitat, temperature and humidity differ along the vertical axis from the ground to the canopy, as revealed by digital thermohygrometers (HOBO H8 Pro, Onset) placed at three different heights (Wells 2002) (Fig. 1 a, b). The lowland rainforest is home to approximately 130 species of non-volant mammals (Payne *et al.* 1998). Despite the extensive and ongoing clearing of forests, remaining forest areas are estimated to cover 50 % of the land, although large proportions of this forest have been subject to high-grade commercial logging (WWF 2005).

We selected a total of six study sites: three in unlogged lowland rainforest and three in logged rainforest, which had been selectively logged *ca.* 15–25 year previous to our study. All sites were situated in northern Borneo (Sabah, Malaysia) at altitudes of 200–900 m above sea level (unlogged forests: Kinabalu National Park at 06°02'N, 116°42'E; Tawau Hills National Park at 04°23'N, 117°53'E; Danum Valley Conservation Area at 04°57'N, 117°48'E; logged forests: Kg. Monggis at 06°13'N, 116°45'E; Kg. Tumbalang at 06°08'N, 116°53'E; Luasong Field

Centre at 04°36'N, 117°23'E). The unlogged forest stands were characterized by relatively undisturbed vegetation with emergent trees up to 60 m tall. Conversely, canopy heights at the logged forest sites reached only *ca.* 25–30 m, with only a few remaining larger trees of no commercial value (e.g., *Ficus* spp.). Compared to unlogged forests, logged forests had pronounced gaps dominated by fast-growing plants, such as climbing bamboo (*Dinochloa* spp.), sago palms (*Metroxylon* spp.), and rattan (*Calamus* spp.).

Between September 2002 and November 2004 small mammals were live-trapped with wire-mesh cage traps baited with banana. We conducted 18 trapping sessions and alternated between the six study sites, leading to a total of three sampling units, each lasting for 16 days, per site. Captured animals were sedated and marked with transponders. Selected individuals were equipped with a spool-and-line device consisting of a quilting cocoon (Danfield Ltd., U.K.) of approximately 120 m of nylon thread encased by a heat-shrunk plastic (total weight approximately 1.7 g), which was glued with cyanoacrylate (Pattex, Henkel, Germany) to the fur between the shoulders. Tracks were followed the next day to investigate habitat use and movement trajectories, until the end of the thread or a nest was found (Wells *et al.* 2006). Additional burrow records for the giant rat *Leopoldamys sabanus* were obtained from radio-tracking data.

For all nests, we recorded the nest type, utilised construction material, and characters of the surrounding environment, if applicable.

TABLE 1. Number of subterranean and above-ground nests found for seven species of non-volant small mammals in Borneo. Body mass of all adults captured throughout the study are given with the number of individuals (n) in parenthesis.

Species Scientific name	Common name	Family	Body mass (g)	Sub-terranean nests	Above-ground nests
Leopoldamys sabanus	Long-tailed giant rat	Muridae	368 ± 64 (n = 101)	20	4
Maxomys rajah	Brown spiny rat	Muridae	160 ± 35 (n = 28)	21	2
Maxomys surifer	Red spiny rat	Muridae	157 ± 47 (n = 38)	12	1
Niviventer cremoriventer	Long-tailed tree rat	Muridae	69 ± 13 (n = 142)	2	4
Sundasciurus lowii	Low's squirrel	Sciuridae	96 ± 22 (n = 24)	1	4
Tupaia longipes	Common treeshrew	Tupaiidae	196 ± 25 (n = 59)	–	2
Tupaia tana	Large treeshrew	Tupaiidae	218 ± 27 (n =126)	1	6
Total				56	24

RESULTS

We recorded 83 nest sites of seven species of small mammals (Table 1). Sample sizes for the different species did not permit the use of statistics to determine the influence of forest types on nesting patterns. However, all nests made of plant fibers and leaves, as described below, were found in logged forest near vegetation typically abundant in logged forests, such as *Metroxylon* palms and *Dinochloa* bamboo. Locations of all nests appeared to be independent of vegetation cover for all species, since we observed nests concealed within dense undergrowth and others where there was little understory cover.

Maxomys rajah/surifer. Nests of spiny rats of the genus *Maxomys* were mostly subterranean (33 out of 36), with no observed differences in nest characteristics between the similar species *M. rajah* and *M. surifer*. Thus we describe nest characteristics/attributes together for both species.

Only three nests were above ground: two were in hollow logs of 10–25 cm diameter, and the third was inside a hollow root of an emergent tree. From inside the subterranean burrows, we retrieved uncoiled sections of threads of up to 2.2 m before finding a ball of thread, indicating a distance of about 2 m to the chamber of the burrow.

Most burrows (65 %, 15 out of 23 for *M. rajah* and 7 out of 11 for *M. surifer*) were most probably self-made with round entrance holes 4–6 cm in diameter. In eight records, we found spiny rats entering two different entrances/burrows. Both species covered entrance holes with leaves from inside their burrows (Fig. 2).

Leopoldamys sabanus. We located 24 nests of *L. sabanus* by spool-and-line and radio-tracking. Twenty nests were subterranean, of which four were located close to a stream, with partly wet ground inside (Fig. 3). The smallest entrance hole was 40 mm in diameter,

FIG. 2. Subterranean burrow of *Maxomys rajah*. The nylon thread leads inside the burrow and the entrance is covered by leaves.

FIG. 3. Subterranean burrow of *Leopoldamys sabanus*. The entrance is located near a stream, and the inside of the burrow is wet after several days of rain.

whereas most (13 out of 20) entrances were between 50 and 80 mm in diameter. One burrow had 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 fibers formed into a pad in a cavity below a dense stand of climbing bamboo *Dinochloa* spp. in a logged forest. In two instances, we observed an adult male sharing a burrow with an adult female. In one case, a female was recorded sharing a burrow with a juvenile, and in another case two juveniles were observed sharing a burrow. Up to four juveniles were recorded in the proximity of the same burrow. A spiny rat (*M. rajah/surifer*) entered a burrow that had been previously occupied by an immature giant rat (*L. sabanus*) 12 days before.

Niviventer cremoriventer. We recorded six nests of the arboreal rat *N. cremoriventer*. Only two nests were subterranean, another two were under dense clusters of logs and branches, and two were 1–1.5 m above the ground. One above-ground nest measured 10 x 10 x 15 cm and was woven from leafs of *Dinochloa* sp. with an entrance funnel made of around 10 leaves. The other above-ground nest was made of rotten plant fibers (probably from *Metroxylon* sp.), hanging from a branch of a sapling (Fig. 4). We observed two litters of four newborns.

Sundasciurus lowii. We discovered five nests of the scansorial squirrel *S. lowii*. Of these, one was subterranean, with an entrance hole of 6 cm in diameter, near an emergent tree.

Two nests were in tree cavities: one in an emergent tree at a height of 2 m with nest material of leaves and plant fibers inside, the other at a height of 0.5 m in a stump. Two nests consisted of 10–15 cm-diameter balls of woven plant fibers and leaves, at heights of 2 and 3.5 m between branches of *Metroxylon* palms.

Tupaia longipes. We observed only two nests for the treeshrew *T. longipes*. One was located under a dense cluster of dead branches covered additionally with loose leaves. Another was in a tree cavity 10 cm in diameter, at a height of 1.1 m.

Tupaia tana. Of seven nests observed for *T. tana*, five were underground cavities at the base of large tree

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FIG. 4. Above-ground nest of *Niviventer cremoriventer* made of woody fiber.

roots. A sixth nest was a cavity in the ground below a rotten log. The seventh nest, inhabited by a male, was woven of plant fibers, and was very similar to the nests described for *S. lowii* (see above). It was fixed between *Metroxylon* branches at a height of *ca.* 1.5 m (Fig. 5).

DISCUSSION

Our study documents distinctive patterns of nest location and construction for the seven species studied. In general, we were able to distinguish among five overall types of nest: 1) self-made subterranean burrows, 2) ground cavities with natural entrances between the soil and roots or rocky crevices, 3) nests below dense accumulations of woody debris, 4) tree cavities, and 5) above-ground nests made of woody fiber or leaves. Although our small sample size only provides limited insight into nest location and construction, the observed patterns suggest that nesting

behavior largely reflects species' space use. For example, species that forage on the ground nested mostly below ground, whereas the number of nests above ground increased with the tendency of a species to forage in trees (Emmons 2000, Wells *et al.* 2006). The terrestrial spiny rats *M. rajah* and *M. surifer* were found to nest exclusively in subterranean burrows or in natural cavities with entrances on the ground. The terrestrial rat *L. sabanus*, which undertakes occasional forays into the canopy, used mostly subterranean burrows but some above ground. Conversely, the arboreal rat *N. cremoriventer* was the only rat species that repeatedly used nests above ground. Similarly, the above-ground location of nests of *S. lowii* and the treeshrews *T. longipes* and *T. tana* reflect their scansorial activity. Consistent with these observations, Emmons (2000) recorded nesting sites of the arboreal treeshrews *T. minor* and *Ptilocercus lowii* well above ground, whereas the arboreal mouse *Chiropodomys major* seems to

inhabit cavities at ground level and also higher in trees (Wells *et al.* 2004a,b).

These nesting patterns are not only of interest with respect to the spacing patterns of these species within this speciose community, but also because of the different structural and floristic requirements necessary to ensure nest establishment, which in turn may influence small mammal density. The distinctive nesting patterns among species indicate that they differ in their requirements of structural and compositional aspects of the rainforest environment for the establishment of suitable nesting sites. Self-made subterranean burrows would depend more on the animals' digging capabilities rather than the available material. Conversely, nests of leaves or woody fibers above ground level require particular materials for construction, suitable branch texture for nest suspension, and runways for efficient access and escape. Furthermore, the availability of tree cavities depends largely on the type of forest stand (e.g., DeWalt *et al.* 2003). This might be particularly important for treeshrews as they frequently change their daily refuges (Emmons 2000). They are known to utilize a large range of material for nesting, and are also likely to use abandoned refuges from squirrels or birds (Martin 1968, Emmons 2000). This idea is supported by our results, as refuges made of woody debris occupied by *T. tana* and *S. lowii*, which were located at the same logged forest site, were similar in the type of architecture and size. Conversely, rats of the genera *Maxomys* and *Leopoldamys* were frequently observed returning to the same subterranean burrows (K. Wells,

FIG. 5. Nest of *Tupaia tana* anchored between a tree trunk and branches of a *Metroxylon* palm.

pers. obs.). Presumably, these rats use a long-term housing strategy despite environmental variation (e.g., the presence of fruit resources) in the vicinity of nest sites. This is also supported by observations that spiny rats consume and/or store seeds (e.g., hard-shelled *Lithocarpus*) inside their burrows (Wells & Bagchi 2005), presumably for later consumption. Although construction of subterranean burrows requires considerable energy expenditure, it may reduce predation risk and provide the small mammal with increased independence from external conditions (Nevo 1979). The vertical distance from the ground to the nest, and its exposure to sun and rain, might also influence small mammal energetic aspects, because average temperature increases with height, while relative humidity decreases along the vertical axis (Fig. 1 a, b). Such considerations are of particular concern with respect to the ongoing human-caused forest degradation, which affects habitat conditions for many animals (DeWalt *et al.* 2003). Negative effects of logging on nesting, because of differences in structure and available material, have been reported, for instance, for tropical marsupials (Laurance 1990), mouse lemurs (Ganzhorn & Schmid 1998), and orangutans (Ancrenaz *et al.* 2004), despite their flexibility in nesting requirements. We were not able to record any differences between logged and unlogged forest sites, possibly because of the small samples sizes of above-ground nesting species that would have been expected to be most strongly affected. However, all nests made of woody fiber were found in logged forests and were likely to include material from the sago palm *Metroxylon*, which was usually abundant close to these nests but much less common in unlogged forests (K. Wells, pers. obs.). Logged forests are also depauperate in downed woody debris such as large hollow logs and stumps (DeWalt *et al.* 2003), which may serve as denning sites for many species (McCay 2000). The effects of logging on nests reach beyond the initial impacts on population density of a particular small mammal species, as nesting conditions might affect interspecific interactions with predators and parasites. Differences in predation rates for different nest types and habitats, for example, have been recorded for birds (e.g., Remeš & Martin 2002, Martin & Joron 2003). Moreover, nesting patterns should receive more attention in studies investigating host-parasite interactions in the context of unravelling the infestation patterns of particular small mammal species and how these relationships are altered in modified forest environments. Fleas (Siphonaptera) collected from *T. ta-*

na and *S. lowii*, for instance, were congeneric *Medwayella* species (Beaucournu & Wells 2004), congruent with the likely overlap in nest utilization of the two host species. Further, gastrointestinal parasite assemblages (specifically Nemathelminthes), in which direct transmission of species depends on frequent host interactions, were found to be influenced by habitat modifications (K. Wells, unpublished data; see also Gillespie *et al.* 2005). The role of nest characteristics and the plasticity in nesting behavior of different species remain largely unknown for the tropics. Our comprehension of the interplay of small mammals with their environment should be improved by future research on small mammal nesting behavior, which may clarify the role of nesting patterns in shaping small mammal populations subject to different local conditions.

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