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SHORT COMMUNICATION

Seed consumption by small mammals from Borneo

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Fruit and seed consumers can both positively and negatively affect plant recruitment through seed dispersion and seed predation, respectively. In turn, fruits influence the abundance and distribution of consumers sustained by local plant assemblages. These interactions are key processes in plant recruitment and the dynamics of tropical forests, where most plants depend on dispersal by frugivorous animals (Corlett 1998). An understanding of these interactions and the functional role of particular seed-dispersing animals is increasingly important nowadays, given that human impact on tropical forest ecosystems may negatively impact seed dispersal and forest regeneration in both natural and human-altered forests (Wright *et al.* 2000).

Small mammals generally comprise species-rich and abundant assemblages in tropical forests that exploit various habitats on the ground and in the different strata above (Bourlière 1989, Malcolm 1991, Voss & Emmons 1996, Wells *et al.* 2004). Most of the commonly encountered small mammals in South-East Asian forests are considered to have an omnivorous and opportunistic diet, including a wide array of plant and animal materials (Emmons 1991, Langham 1983, Leighton & Leighton 1983, Lim 1970). However, detailed information on diet composition and the types or quantities of seeds being consumed are rarely available, and the presumably important role of small mammals as seed dispersers remains anecdotal and has yet to be quantified.

Generally, the majority of studies on small mammals and seeds have been centred on seed dispersal via scatterhoarding fruits (Asquith *et al.* 1997, Blate *et al.* 1998, Brewer & Rejmánek 1999, Forget & Milleron 1991, Guariguata *et al.* 2000, Hoch & Adler 1997, Vieira *et al.* 2006, Wells & Bagchi 2005, Yasuda *et al.* 2000). Little information is available on the diversity and quantity of seeds that are swallowed and defecated by a large number of animals within consumer assemblages. In particular, there is not only a lack of knowledge of which seeds might be dispersed this way but also on the relative contribution of different small-mammal species to seed dispersal. In this study, seed contents were examined in 701 faecal samples from 13 non-volant small-mammal species in rain forests in Borneo (Sabah, Malaysia).

Small mammals were captured in three old-growth forest sites (Danum Valley Conservation Area, Kinabalu National Park, Tawau Hills Park) and three logged forests (Kampung Monggis, Kampung Tumbalang, Luasong) located at distances between 17–236 km from each other. We conducted a total of 16 trapping efforts lasting 16 d each, continuously alternating between the various forest sites between September 2002 and November 2004 (Wells *et al.* 2007). Faeces from first captures of permanently marked individuals were collected from the floor below the trapped animals and stored in 3% formalin. Small-mammal faecal samples from the families Muridae, Sciuridae and Tupaiidae (Table 1) were screened under a light microscope and all visible seeds extracted. All seed samples were photographed to aid in classification and information exchange with other research groups. As we were unable to identify most seeds, they were assigned to different classes based on their size, shape, colour and surface.

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Table 1. Seed content in faecal samples from non-volant small mammals captured in various logged and unlogged forest sites in northern Borneo. Body masses of adults are given as the mean proportions of body mass with 1 SD of individuals captured (number of individuals for each species is given in parentheses) as part of the entire trapping effort (Wells *et al.* 2007).

Species	Body mass (g)	Number of samples examined	Number of samples with seeds	Proportion of samples containing seeds	Largest seed size swallowed (mm)
Muridae					
Leopoldamys sabanus (Thomas 1887)	368 ± 64 (101)	145	48	0.33	3.6
Sundamys muelleri (Jentink 1879)	204 ± 29 (27)	22	6	0.27	1.8
Maxomys rajah (Thomas 1894)	160 ± 35(28)	66	14	0.21	1.5
Maxomys surifer (Miller 1900)	157 ± 47 (38)	50	10	0.20	2.1
Maxomys cf. *surifer/rajah*	–	32	3	0.09	–
Rattus rattus (Linnaeus 1758)	113 ± 18 (2)	1	–	–	–
Niviventer cremoriventer (Miller 1900)	69 ± 13 (142)	111	23	0.21	3.2
Maxomys baeodon (Thomas 1994)	60 ± 7 (2)	1	1		–
Maxomys whiteheadi (Thomas 1894)	53 ± 11 (30)	34	1	0.01	1.1
Sciuridae					
Sundasciurus lowii (Thomas 1892)	96 ± 22 (24)	9	2	0.22	0.7
Tupaiidae					
Tupaia tana (Raffles 1821)	218 ± 27 (126)	95	14	0.15	2.5
Tupaia longipes (Thomas 1893)	196 ± 25 (59)	90	14	0.16	5.8
Tupaia gracilis (Thomas 1893)	81 ± 19 (14)	1	–	–	–
Tupaia minor (Günther 1876)	58 ± 9 (31)	44	2	0.05	0.6
Total		701	138	0.20	

In total, 138 out of 701 faecal samples contained seeds (Table 1), from 13 species of small mammal. We were able to divide seed samples into at least 11 different seed morphotypes. Specific seed identification was not possible, as seeds from faeces and those extracted from known fruits were not comparable. Faecal samples from rats contained seeds significantly more often (106 out of 462; 23%) than samples from tree shrews (30 out of 230; 13%) ($\chi^2 = 6.08$, df = 1, $P < 0.05$).

We found significantly fewer seeds in samples from the rat *Maxomys whiteheadi* compared with *Leopoldamys sabanus*, while we were not able to reveal any differences in seed incidences for other species pairs. However, the relatively low sample sizes together with low powers of most performed chi-square tests urges for caution when interpreting the lack of differences in the proportions of samples with/without seeds across species.

Seeds of figs (*Ficus* sp.) were present in 74 out of 701 samples (11%), including samples from all commonly caught species with the exception of *Tupaia minor*. These fig seeds were around 0.5–1 mm in width and 0.4–1 mm in length with a yellowish colour. Another seed type occurred in 28 samples (4%). These seeds were around 2.5–3.5 mm in width and 2.5–6 mm in length with a brown seed coat and a white endosperm. This seed type appeared to be intact in faecal samples from the rat *L. sabanus* and the two larger tree shrews *T. longipes* and *T. tana*, while it usually occurred in fragments in samples from the medium- to small-sized rats *M. rajah*, *M. surifer* and *Niviventer cremoriventer*.

Overall seed incidences in faecal samples from logged forests were significantly greater than in unlogged forests for the rats *L. sabanus* and *M. rajah* (both $\chi^2 > 7.27$, df = 1, $P < 0.01$). However, there was no obvious difference in the occurrence of specific seed types in samples from either forest type.

These results show that small mammals such as rats and tree shrews contribute to seed consumption in South-East Asian forests. In particular, our faecal screening revealed that a considerable number of samples contained seeds between 0.5 mm to 5 mm in diameter, with fig seeds being most frequent amongst the commonly caught small-mammal species. The frequent prevalence of fig seeds in faeces confirm that figs serve as an important fruit resource for small mammals (Shanahan & Compton 2000). The occurrence of seeds in 23% of rat samples analysed suggests that rats might play a more important role in seed dispersal in tropical forests than previously assumed (Shanahan *et al.* 2001, Vieira *et al.* 2006). In fact, rats comprise most individuals and species within small-mammal assemblages on both the ground and in the canopy of tropical forests (Adler 2000, Bourlière 1989, Malcolm 1991, Voss & Emmons 1996, Wells *et al.* 2004). Such a ubiquitous presence, together with diverse rat assemblages of species that explore the forest throughout its three-dimensional space, should thus comprise a suitable prerequisite for efficient seed dispersal.

However, our results are preliminary lacking exact seed identification and not knowing which seeds were viable or not. Despite this limitation, the recorded seed contents suggest that specific characteristics of small-mammal species as well as the type of forest may impact patterns of seed consumption.

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The larger seed content in faeces from rodents compared with tree shrews was expected due to their more general feeding behaviour and physiology. The strong incisors of rats and other rodents allow them to feed on hard-shelled fruits such as *Parashorea* (Dipterocarpaceae) and *Lithocarpus* (Fagaceae) (Wells & Bagchi 2005, Yasuda *et al.* 2000). In contrast, tree shrews are well known to feed mostly on soft-shelled fruits such as figs (*Ficus* sp.), as their relatively weak jaws and teeth likely limit the consumption of hard fruits and seeds (Emmons 1991, 2000; Shanahan & Compton 2000). Notably, the simple digestive tract of tree shrews leads to quick food transition with estimated retention times as short as 20–60 min (Emmons 1991), limiting the dispersal distances between food consumption and defecation (Kalko *et al.* 1996). Additionally, species-specific characteristics such as eating behaviour and body size may influence the fate of consumed seeds. For example, we found more destroyed and fragmented seeds in faeces of small to medium-sized rat species (e.g. *Maxomys* sp. and *Niviventer cremoriventer*), while the same seed type was found intact in samples from the larger rat *Leopoldamys sabanus*. Although our knowledge on specific interactions between small mammals and seeds is rather poor, the overall significance of small mammals and the differing potential of species as seed dispersers is of much interest with regard to large-scale forest changes by logging. While the altered abundance or species composition of small-mammal assemblages might influence seed dispersal of plant species in logged forests, different plant composition in disturbed forests, in turn, may influence fruit availability for small mammals. The observed increases in overall seed defecation by two rats, for example, suggest that logging influences the proportion of fruits in the diet of some small-mammal species. Our tentative results, with a lack of seed identification and detailed insights into animal–seed interactions, act more to highlight some gaps in our knowledge rather than solve these issues. Logged forests are known to differ in tree and overall plant composition and thus also in the availability of food resources (Bischoff *et al.* 2005, Howlett & Davidson 2003). To date there is little consensus on the result of logging on fruit availability and fruit consumption patterns by vertebrates (Heydon & Bulloh 1997, Knop *et al.* 2004, Lambert *et al.* 2005). In other study locales, altered vertebrate populations and defaunation reduced seed recruitment (Asquith *et al.* 1997, Guariguata *et al.* 2000, Wright *et al.* 2000).

More detailed data on seed consumption patterns in terms of specificity and strength of interactions in different forests are needed in order to draw conclusions on how interactions between small mammals and seeds pay off for each other in this mutualistic relationship and how they contribute to ecosystem maintenance.

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LITERATURE CITED

ADLER, G. H. 2000. Tropical tree diversity, forest structure and the demography of a frugivorous rodent, the spiny rat (*Proechimys semispinosus*). *Journal of Zoology* 250:57–74.

ASQUITH, N. M., WRIGHT, S. J. & CLAUSS, M. J. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology* 78:941–946.

BISCHOFF, W., NEWBERY, D. M., LINGENFELDER, M., SCHNAECKEL, R., PETOL, G. H., MADANI, L. & RIDSDALE, C. E. 2005. Secondary succession and dipterocarp recruitment in Bornean rain forest after logging. *Forest Ecology and Management* 218:174–192.

BLATE, G. M., PEART, D. R. & LEIGHTON, M. 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* 82:522–538.

BOURLIÈRE, F. 1989. Mammalian species richness in tropical rainforests. Pp. 153–168 in Harmelin-Vivien L. & Bourlière F. (eds.) *Vertebrates in complex tropical systems*. Ecological Studies 69. Springer, New York.

BREWER, S. W. R. & REJMÁNEK, M. R. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science* 10:165–174.

CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews of the Cambridge Philosophical Society* 73:413–448.

EMMONS, L. H. 1991. Frugivory in tree shrews (*Tupaia*). *American Naturalist* 138:642–649.

EMMONS, L. H. 2000. *Tupai: a field study of Bornean treeshrews*. University of California Press, Berkeley, Los Angeles. 269 pp.

FORGET, P.-M. & MILLERON, T. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87:596–599.

GUARIGUATA, M. R., ROSALES, A. J. J. & FINEGAN, B. 2000. Seed removal and fate in two selectively logged lowland forests with contrasting protection levels. *Conservation Biology* 14:1046–1054.

HEYDON, M. J. & BULLOH, P. 1997. Mousedeer densities in a tropical rainforest: the impact of selective logging. *Journal of Applied Ecology* 34:484–496.

HOCH, G. A. & ADLER, G. H. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology* 13:51–58.

https://doi.org/10.1017/S0266467409990058 Published online by Cambridge University Press

HOWLETT, B. E. & DAVIDSON, D. W. 2003. Effects of seed availability, site conditions, and herbivory on pioneer recruitment after logging in Sabah, Malaysia. *Forest Ecology and Management* 184:369–383.

KALKO, E. K. V., HERRE, E. A. & HANDLEY, C. O. 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography* 23:565–576.

KNOP, E., WARD, P. I. & WICH, S. A. 2004. A comparison of orang-utan density in a logged and unlogged forest on Sumatra. *Biological Conservation* 120:183–188.

LAMBERT, T. D., MALCOLM, J. R. & ZIMMERMAN, B. L. 2005. Effects of mahogany (*Swietenia macrophylla*) logging on small mammal communities, habitat structure, and seed predation in the southeastern Amazon Basin. *Forest Ecology and Management* 206:381–398.

LANGHAM, N. 1983. Distribution and ecology of small mammals in three rain forest localities of Peninsula Malaysia with particular references to Kedah Peak. *Biotropica* 15:199–206.

LEIGHTON, M. & LEIGHTON, D. R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp. 181–196 in Sutton S. L., Whitmore T. C. & Chadwick A. C. (eds.). *Tropical rainforests: ecology and management*. Blackwell Science, Oxford.

LIM, B. L. 1970. Distribution, relative abundance, food habits and parasite patterns of giant rats (*Rattus*) in West Malaysia. *Journal of Mammalogy* 51:730–740.

MALCOLM, J. R. 1991. Comparative abundances of neotropical small mammals by trap height. *Journal of Mammalogy* 72:188–192.

SHANAHAN, M. & COMPTON, S. G. 2000. Fig-eating by Bornean tree shrews (*Tupaia* spp.): evidence for a role as seed dispersers. *Biotropica* 32:759–764.

SHANAHAN, M., SO, S., COMPTON, S. G. & CORLETT, R. T. 2001. Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* 76:529–572.

VIEIRA, E. M., PAISE, G. & MACHADO, P. H. D. 2006. Feeding of small rodents on seeds and fruits: a comparative analysis of three species of rodents of the *Araucaria* forest, southern Brazil. *Acta Theriologica* 51:311–318.

VOSS, R. S. & EMMONS, L. H. 1996. Mammalian diversity in neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American Museum of Natural History* 230:1–115.

WELLS, K. & BAGCHI, R. 2005. Eat in or take away – seed predation and removal by rats (Muridae) during a fruiting event in a dipterocarp rainforest. *Raffles Bulletin of Zoology* 53:281–286.

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.

WELLS, K., KALKO, E. K. V., LAKIM, M. B. & PFEIFFER, M. 2007. Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia. *Journal of Biogeography* 34:1087–1099.

WRIGHT, S. J., ZEBALLOS, H., DOMINGUEZ, I., GALLARDO, M. M., MORENO, M. C. & IBANEZ, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* 14:227–239.

YASUDA, M., MIURA, S. & HUSSEIN, N. A. 2000. Evidence for food hoarding behaviour in terrestrial rodents in a Malaysian lowland rainforest. *Journal of Tropical Forest Science* 12:164–173.

https://doi.org/10.1017/S0266467409990058 Published online by Cambridge University Press