

## EAT IN OR TAKE AWAY – SEED PREDATION AND REMOVAL BY RATS (MURIDAE) DURING A FRUITING EVENT IN A DIPTEROCARP RAINFOREST

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**Abstract.** – Seed predators are considered important in the evolution of mast fruiting. Mast events in turn provide an abundant food resource for consumers, but only for a limited period of time. In this study seed removal experiments, feeding trials and small mammal trapping were used to determine the potential of forest rats (Muridae) as predators and dispersers of two tree species, *Lithocarpus gracilis* (Fagaceae) and *Parashorea malaanonan* (Dipterocarpaceae) during a minor fruiting event in a dipterocarp rainforest at Danum Valley (Sabah, Malaysia) in Sept/Oct 2004. Seeds of both species were exploited by rodents at similar frequencies. Nearly all seeds exploited were removed from the feeding stations. Seeds placed near burrows of *Maxomys rajah* were moved into the burrows. Gnawed seeds collected in fruit fall traps (8% of total collected) indicated that *Parashorea* seeds were also exploited in the canopy. Partially eaten seeds often retained their ability to germinate. Captive rats ate a range of dipterocarp and other hard-shelled seed and feeding on an individual seed could take up to 27 minutes. Trap success for rats, but not tree shrews (Tupauidae) and civets (Viverridae), decreased during the fruiting season. This supports the idea that this group benefits from mast fruiting. Rats are evidently important predators of the seeds of these tree species, both before and after dispersal. However, due to the removal of seeds before eating, long consumption times and the ability of partially consumed seeds to germinate, they may also function as secondary dispersal agents.

**KEY WORDS.** – Seed dispersal, scatter hoarding, predator satiation, *Parashorea*, *Lithocarpus*, *Maxomys*.

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### INTRODUCTION

Fruit production in tropical forests is highly variable through time and often occurs in synchronised “mast” events (Curran et al., 1999; Leighton & Leighton, 1983; Smythe, 1986). In southeast Asian dipterocarp rainforests, mast fruiting has been well reported as a community-wide event including seeds of the Dipterocarpaceae but also other species with different fruit phenology (Ashton et al., 1988; Curran & Leighton, 2000; Sakai, 2002). However, the degree of synchrony between trees in fruiting may range from a few individuals of one tree species to a diverse community of various taxa and fruit types. Several species that participate in mast events also produce fruit at other times, with some fruit produced throughout the year. The pay off for any specific pattern of synchrony and quantity in fruiting will depend on 1) interactions with the abiotic environment (Kelly, 1994; Kelly & Sork, 2002; Sakai, 2002); 2) fruit characteristics (e.g. size, protection; Janzen, 1971); 3) interactions with other fruiting species (Curran & Leighton, 2000) and 4) dynamic interactions with the consumer and disperser communities (Kelly, 1994; Kelly & Sork, 2002).

Several hypotheses have been suggested to account for the evolution of mast fruiting (Kelly, 1994). Of these, the most widely accepted suggests that synchronous fruiting evolved to satiate seed predators allowing greater per capita recruitment (Janzen, 1971, 1974; Kelly, 1994; Curran & Leighton, 2000; Kelly & Sork, 2002; Sakai, 2002). Dipterocarp seeds (we use the term ‘seed’ rather than ‘fruit’ for dipterocarp and lithocarp seeds that comprise a nutritious endosperm essential for the germination, except if fleshy fruits are included in the argumentation) are an easily accessible and energy-rich food resource with thin testa that are attractive to *Sus barbatus* (bearded pigs) and possibly to several rodents. Reproductive success of this vulnerable seed type is increased by predator satiation via masting and also by rapid germination of the lipid-rich seeds within one week (Curran & Webb, 2000). Abundant fruit crops are simultaneously produced by *Lithocarpus* (stone oaks), comprising another important element of dipterocarp forests (Cannon & Manos, 2003). *Lithocarpus* fruit every year, and so are not considered masting species (Sakai et al., 1999). The structure of hard-shelled nuts in a fused cupule should provide protection against predation of these seeds. Meanwhile the long

germination period of one to nine months (Ng, 1991) both increases the exposure to consumers and makes them suitable for caching. Caching by rodents appears likely though not yet fully proven (see Corlett, 1998) and may further increase resource utilisation in time.

However, seed fates and the diversity of seed consumers are little investigated for Oriental tropical rainforests (see Blate et al., 1998; Wong et al., 1998; Sodhi et al., 2003), whereas seed predation and dispersal by diverse rodent assemblages has been frequently recorded for Neotropical forests (e.g. Fleming, 1979; Asquith et al., 1997; Hoch & Adler, 1997; Brewer & Rejmanek, 1999; Charles-Dominique et al., 2003). Rats (Muridae) are abundant and omnivorous forest dwellers in various strata of dipterocarp rainforests (Harrison, 1962; Wells et al., 2004), yet their role as seed predators and dispersers have been little investigated (but see Blate et al., 1998; Curran & Leighton, 2000). Their effective utilisation of three-dimensional space in the forest suggest great potential for seed predation in space and time due to arboreal foraging and possible caching. However, as rats are also exposed to carnivore predators during feeding, their seed handling and consumption time is also subject to constraints. The constitution and nutritional value of different seeds types should determine the handling time, proportion of consumption of a single seed, and whether seeds are removed. Different seed characters and distributions should thus specifically influence resource exploitation and resulting seed fate, and hence may be an important proximate determinant of satiation strategies. Here we report on a seed fate study and feeding observations in order to estimate the role of rats as predator and dispersal agents on two seed types (*Parashorea* and *Lithocarpus*) that were both commonly available during a dipterocarp fruiting event in a Bornean rainforest.

## MATERIALS AND METHODS

This study was conducted at the Danum Valley Conservation Area (4°57.800'N 117°48.173'E), Sabah, Malaysia. The conservation area includes more than 43,000 ha of lowland evergreen rainforest and is surrounded by 973,000 ha of selectively logged forest. The vegetation is dominated by the Dipterocarpaceae in the canopy and Euphorbiaceae in the understorey (Newberry et al., 1992; Marsh & Greer, 1992). A partial dipterocarp mast-fruiting event occurred in September – November 2004. The principle species involved were *Parashorea malaanonan* (Merr.), *Shorea leprosula* (Miq.), and *S. parvifolia* (Dyer.). Fruits were also available from several species that fruit more regularly including *Lithocarpus gracilis* (Korth.) Soepadmo (Fagaceae), several *Ficus* species (Moraceae), several Euphorbiaceae and Rubiaceae among others. *P. malaanonan* and *L. gracilis* fruits were particularly abundant.

A seed choice and removal experiment was conducted with two types of seeds: *P. malaanonan* (mean weight = 5.0 g ± 0.10,  $n = 292$ ) and *L. gracilis* (mean weight = 3.1 g ± 0.7,  $n = 90$ ). Seeds with no signs of predation or germination were

collected from the forest floor. A thin thread with a coloured flag was attached to each seed, wined between fruit and sepals/cupules, respectively, and 55 experimental stations consisting of one seed of each species were arranged linearly 2-3 m apart in two areas (505 station nights in total). Further seed stations (three per burrow) were established near burrows of *Maxomys rajah* (Thomas.) ( $n = 2$ ) that were located beforehand. Each station was monitored daily for up to 11 days. Disappeared or damaged seeds were replaced upon each check and the germination of non-removed seeds was recorded. We considered seeds found less than 50 cm away from the original position as displaced, seeds not found within 50 cm as removed. The selective removal of only single seeds, remains of gnawed off sepals or cupules or cracked seeds with incisor marks were considered to indicate rodents as the most likely predators. A removed seed could have either been predated or dispersed, but we were not able to distinguish between the two.

A juvenile *Maxomys* cf. *rajah/surifer* and a female adult *Maxomys whiteheadi* (Thomas.) were kept in captivity for three to four days for feeding observations before release at the place of capture. Fruit of various species (*Neoscortechinia* sp. (Euphorbiaceae), *Shorea fallax*, *S. leprosula*, *S. parvifolia*, *P. malaanonan*, *Dryobalanops lanceolata* (all Dipterocarpaceae), *L. gracilis* (Fagaceae), *Aglaia elliptica* (Meliaceae), four species of *Ficus* sp. (Moraceae) and *Tetrastigma* sp. (Vitaceae)) were offered simultaneously every evening. Feeding was observed continuously for the first hour of each trial, after which the rat was left undisturbed except for periodic cleaning and provisioning with clean water. During the first hour, the time spent eating fruit of each species exploited and any movement of fruit were recorded. At the end of every trial, the number of fruit of each species consumed was noted. Damaged or consumed fruit were then replaced for the start of the next trial. Damaged fruit were placed on moist tissue paper to assess their viability. Seeds were checked for the presence of a radical every two days for a period of one month after collection.

To assess rodent predation on dipterocarp seeds in the canopy, seed damage was recorded for seeds gathered with seed traps placed near fruiting *P. malaanonan*. We established seed traps in at distances of 2, 10, 20, and 30 meters along a transect line at ten separate trees with large fruit crops. Seeds from the traps were gathered every four days for a period of 2 months. Seeds were classed as undamaged, potentially viable (more than half of the seed remaining) or predated (seeds were more than half consumed or cracked into pieces). Potentially viable seeds were put on moist tissue paper in the laboratory to monitor germination ability as outlined above.

To compare the trap success of rats and other small mammals between the fruiting season in September – October 2004 and other seasons, locally made cage traps (28 x 14 x 14 cm) baited with ripe banana were placed for 16 consecutive days on the forest floor in March and December 2003 and in September – October 2004, comprising a total trapping effort of 5,967 trap nights. During the seed fall period, *P.*

Table 1. The fate of seeds exploited by rodents at 55 feeding stations (505 station nights in total).

	<i>Parashorea</i>	<i>Lithocarpus</i>
Eaten at station	3	0
Displaced	1	7
Removed	5	4
Total	9	11

Table 2. Proportion of consumed seeds and 'explored' seeds that were removed or found with gnawed off wings or radicals in a feeding choice experiment. Data are pooled for all trials. Maximum handling times [min.] of seeds are given in brackets. Feeding trials lasted for four nights for *M. rajah/surifer* and three nights for *M. whiteheadi* with four fruits of each species offered.

Species	Family	<i>M. cf. rajah/surifer</i>		<i>M. whiteheadi</i>	
		Consumed	Explored	Consumed	Explored
<i>Neoscortechinia forbesii</i>	Euphorbiaceae	0.81	0	0.08	0.08
<i>Lithocarpus gracillius</i>	Fagaceae	0.13	0.38	0.17	0.25
<i>Dryobalanops lanceolata</i>	Dipterocarpaceae	0	0	0	0
<i>Parashorea malaanonan</i>	Dipterocarpaceae	0.50 (27)	0.25	0.08	0.66
<i>Shorea fallax</i>	Dipterocarpaceae	0.25 (10)	0	0.33	0
<i>Shorea leprosula/parvifolia</i>	Dipterocarpaceae	0.41 (4)	0.24	0.91	0
<i>Aglaia elliptica</i>	Meliaceae	0	0	0	0
<i>Ficus</i> sp. (4 species)	Moraceae	0	0	0	0
<i>Tetrastigma</i> sp.	Vitaceae	0	0	0	0

*malaanonan* and *L. gracilis* seeds were placed in some traps to confirm their consumption by small mammals. For a diversity estimate we used the Shannon-Wiener H' index and compared H' between different trapping periods with 10,000 runs by use of the "Species diversity and richness" software (Henderseon & Seaby, 1998).

## RESULTS

Rodents appeared to frequently utilise *P. malaanonan* and *L. gracilis* seeds as a food resource. At the experimental feeding stations, nine *P. malaanonan* (16%) and 11 *L. gracilis* (20%) seeds were exploited (Table 1), most probably by rodents. Consumption of exploited seeds near the place of encounter was low. Only two *P. malaanonan* seeds were completely eaten near (within 50 cm) the feeding station. The radicals of another two *P. malaanonan* seeds were gnawed off. The wings and attached flags were gnawed off the other *P. malaanonan* seeds before removal to an unknown fate. No exploited *P. malaanonan* seeds recovered were viable. While the removal rate was similar for *L. gracilis*, seeds were more frequently displaced (distances between 10-30 cm) and two of these displaced seeds were found buried. No *L. gracilis* seeds were eaten in situ.

Seeds placed in the vicinity of *Maxomys rajah* burrows were moved inside them, indicated by the flags with threads leading down the holes. We recorded four removals of *P. malaanonan* seeds, one removal of a *L. gracilis* seed and one simultaneous removal of two *P. malaanonan* and one *L. gracilis* from near the burrows.

Both *M. rajah* ( $n=1$ ) and *Leopoldamys sabanus* (Thomas.) ( $n=1$ ) consumed the *P. malaanonan* and *L. gracilis* seed provisions placed in traps they were caught in. We were not able to test further species.

A total of 424 seeds were recovered from the seed traps. Out of these, 390 seeds (92 %) were undamaged. A further 18 (4 %) seeds were less than half consumed and potentially still viable, while 16 (4 %) seeds were more than half consumed or cracked into pieces with no further germination ability. Of the 18 half consumed seeds collected, two germinated in the laboratory.

*Maxomys* cf. *rajah/surifer* and *M. whiteheadi* kept in captivity both fed on fruit of all dipterocarps tested (except *D. lanceolata*), *L. gracilis* and *Neoscortechinia* sp.. Fruits of the four *Ficus* species, *A. elliptica* and *Tetrastigma* sp. were rejected by both species (Table 2). During every feeding trial, the rats fed on a mixed fruit diet without finishing the available amount of any single fruit resource. Dipterocarp seeds were moved a short distance from their original position, the sepals gnawed off and feeding on a single seed lasted for up to 27 minutes on one *P. malaanonan* seed. Seeds from *L. gracilis* were frequently hidden under leaves or in corners of the cage while consumption was less than on the available dipterocarp seeds. In most cases, seeds were only partially eaten, and some half-consumed dipterocarp seeds were still able to germinate.

Overall, 188 small mammals (18 species) were captured during the three trapping periods (Table 3). The number of species trapped (range eight to 13 species) and diversity (Shannon-Wiener H', range 1.57 to 1.97,  $p < 0.05$  for all

Table 3. Trap success per 1,000 trap nights for the taxonomic groups of small mammals captured during the three trapping periods. Trap nights per period are given in brackets.

Family	No. of species trapped	No. of individuals per 1,000 trap nights		
		March 2003 (1915)	Dec 2003 (2025)	Sept/Oct 2004 (2027)
Muridae	10	32.37	27.65	4.93
Sciuridae	2	2.09	2.47	0
Tupaiaidae	4	9.40	3.95	9.86
Viverridae	2	0.52	0	1.97
<b>Total</b>	<b>18</b>	<b>44.38</b>	<b>34.07</b>	<b>16.76</b>
Shannon-Wiener H'		1.97	1.84	1.58

comparisons, Table 3) were lowest during the fruiting season in Sept/Oct 2004. The capture of certain species varied between trapping periods. During the fruiting season in Sept/Oct 2004, trap success (individuals/ per trap night) was significantly lower for rats (Pearson's Chi Square:  $\chi^2 = 19.88$ ,  $df = 2$ ,  $p < 0.05$ ). An increased (though not significant) trap success was recorded for tree shrews (Tupaiaidae) and civets (Viverridae) during the fruiting event, indicating that the trap success for rats and other small mammal is influenced by the seasonal availability of abundant fruit resources.

## DISCUSSION

Our results confirm that both terrestrial rats of the genus *Maxomys* and the semi-arboreal *L. sabanus* feed on dipterocarp and lithocarp seeds (see Curran, 1994; Blate et al., 1998; Curran & Leighton, 2000). Much of the literature dealing with dipterocarp fruiting concerns regional mast events (e.g. Curran & Leighton, 2000; Sakai, 2002). Curran and Leighton (2000) suggest that bearded pigs, the most important seed predators in their study, are satiated at the regional rather than local scale. This mechanism is dependent on pigs foraging together in large groups across large areas to feed on dipterocarp seeds (Curran & Webb, 2000), however, a behaviour that was not observed during the fruiting event described here and is probably only triggered by regional masting events. Recent studies in Sabah record some seed survival for a few dipterocarp species even in non-mast years (R. Bagchi, C. Philipson, unpublished data). While bearded pigs were responsible for some seed predation (R. Bagchi, pers. obs.) rodents, which are much less mobile though omnipresent, appeared to be the main seed predators in the study presented here. The predators and hence the scale at which predator satiation occurs may differ in non-mast years or in different localities. Overall, seed predation by rodents may exert a very different selective force on fruiting patterns to that exerted by pigs.

Small seed predators (e.g. rats and squirrels) may be more efficient at foraging for scattered seeds as a single seed will provide proportionally more energy than for larger species (see MacArthur & Pianka, 1966; Smythe, 1986). Collectively, foraging small seed predators are expected to effectively discover most resource patches (Janson & Emmons, 1990;

Beck & Terborgh, 2002). Therefore, rats can be expected to forage on scattered seeds or at the edges of seed shadows in a wide variety of habitat patches that are less attractive or inaccessible to larger mammals like bearded pigs (*Sus barbartus*). Small arboreal species, e.g. the omnivorous and abundant tree rat *Niviventer cremoriventer* (Miller.) (mean weight of adults approximately  $69 \pm 13$  g,  $n = 142$ ), are agile enough to traverse thin distal branches of less than only 2-3 mm in diameter (K. Wells, pers. obs.), where they might explore fruits at an early developmental stage. The small size of rodent seed predators is not only of significance for patterns of seed exploitation on the forest floor but also in three-dimensional space. Our results in combination with these traits further encourage the idea that seed utilisation by rodents is much more extended in space (e.g. arboreal exploitation) and time (e.g. predation on early developmental stages and caching) compared to larger predators.

According to the interfamilial predator satiation hypothesis (Curran & Leighton, 2000) resident seed consumers, like rodents, prefer non-dipterocarp seed resources. As a result, when seeds of other species are abundant, dipterocarps suffer much less predation by residents. However, in this study, resident seed predators appeared to prefer dipterocarp seeds. This may have partly been due to the paucity of other small hard shelled fruit during this period (except for dipterocarps and *Lithocarpus*). Low trap success of common rodents during the fruiting season and a lack of such a change for small mammals probably incapable of consuming dipterocarp seeds (tupaiaids and viverrids) are also consistent with this conclusion.

The exploitation of seeds offered at seed stations revealed no quantitative difference between the exploitation of *Parashorea* and *Lithocarpus* seeds. The majority of seeds exploited from both species were removed from the feeding station. However, seed handling seems to differ as displaced seeds of *Parashorea* were consumed, whereas some displaced lithocarp seeds were buried. The differences in morphology and germination time between the two seed types probably affect the fate of removed seeds, for example the probability of consumption or caching (Forget, 1991; Jansen & Forget, 2001). Dipterocarp seeds germinate very rapidly making them unsuitable for scatterhoarding. In contrast, *L. gracilis* seeds germinate after between 173-178 days (Ng, 1991) making

them more suitable for caching and delayed consumption. The records of buried seeds as well as the seed storing behavior of captive rats make scatterhoarding of *Lithocarpus* seeds by rodents likely. So far, there is very little information available on the extent of caching by rodents and its possible impacts on seed dispersal in Oriental rainforests (Leighton & Leighton, 1983; Corlett, 1998). Despite the differences between the seed types, both seeds may be dispersed inadvertently by rodents moving them. Because *Lithocarpus* seeds are more likely to be cached they will be more likely to be forgotten and survive.

Movement of dipterocarp seeds into burrows or other places is most likely a strategy to consume the seed in a protected place rather than a scatterhoarding activity. Given the potentially long time required for complete consumption of *Parashorea* seeds, a rat would expose itself to a high risk of predation if it consumed the seed at the point of discovery. This movement of seeds will add to the handling time prior to seed consumption, and this may increase the likelihood of local predator satiation.

Studies of caching may also help our understanding of the impact that resource availability has on the population dynamics of seed consumers. Cached seeds, while they extend the availability of the resource for hoarding species, are unavailable to other species. Frugivorous mammals that have been studied in detail show seasonal patterns in population size and reproductive activity, supporting the idea that temporal or limited resource availability is a major force in structuring these populations (Terborgh, 1986; Wolff, 1996; Adler, 1998; Schnurr et al., 2002). We might therefore expect that seed hoarders will show less fluctuation in their population sizes than other species.

At the moment we little understand the interactions between rodent seed predators and their food sources. The absence of large mammals and human disturbance affect small mammal abundances and seed predation (Terborgh, 1986; Asquith et al., 1997; Wright et al., 2000; Caro, 2002; Wyatt & Silman, 2004). Further, variability in tree species composition among forest patches and most severely in secondary forests affects seed availability and predation (Sodhi et al., 2003; Brearley et al., 2004). Rats and squirrels are often the last mammals to remain in disturbed forest fragments (Corlett, 1998). Anthropogenic change could therefore increase the importance of rodent seed predation quite drastically. The potential effect this may have on tree recruitment is unpredictable but is likely to be considerable.

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#### LITERATURE CITED

- Adler, G. H., 1998. Impacts of resource abundance on populations of a tropical forest rodent. *Ecology*, **79**(1): 242-254.
- Ashton, P. S., T. J. Givnish & S. Appanah, 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist*, **132**(1): 44-66.
- Asquith, N. M., S. J. Wright & M. J. Clauss, 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology*, **78**(3): 941-946.
- Beck, H. & J. Terborgh, 2002. Groves versus isolates: how spatial aggregation of *Astrocaryum murumuru* palms affects seed removal. *Journal of Tropical Ecology*, **18**(2): 275-288.
- Blate, G. M., D. R. Peart & M. Leighton, 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos*, **82**(3): 522-538.
- Brearley, F. Q., S. Prajadinata, P. S. Kidd, J. Proctor & Suriantata, 2004. Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. *Forest Ecology and Management*, **195**(3): 385-397.
- Brewer, S. W. & M. Rejmanek, 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science*, **10**(2): 165-174.
- Cannon, C. H. & P. S. Manos, 2003. Phylogeography of the Southeast Asian stone oaks (*Lithocarpus*). *Journal of Biogeography*, **30**(2): 211-226.
- Caro, T. M., 2002. Factors affecting the small mammal community inside and outside Katavi National Park, Tanzania. *Biotropica*, **34**(2): 310-318.
- Charles-Dominique, P., J. Chave, M. A. Dubois, J. J. De Granville, B. Riera & C. Vezzoli, 2003. Colonization front of the understorey palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana. *Global Ecology and Biogeography*, **12**(3): 237-248.
- 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.
- Curran, L. M. 1994. *The ecology and evolution of mast-fruiting in Bornean Dipterocarpaceae: a general ectomycorrhizal theory*. Ph.D. Thesis. Princeton University.
- Curran, L. M., I. Caniago, G. D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C. E. Nirarita & H. Haeruman, 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science*, **286**(5447): 2184-2188.
- Curran, L. M. & M. Leighton, 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**(1): 101-128.

- Curran, L. M. & C. O. Webb, 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**(1): 129-148.
- Fleming, T. H., 1979. Do tropical frugivores compete for food? *American Zoologist*, **19**: 1157-1172.
- Forget, P. M., 1991. Scatterhoarding of *Astrocaryum paramaca* by *Proechymis* in French Guiana: comparison with *Myoprocta exilis*. *Tropical Ecology*, **32**: 155-167.
- Harrison, J. L., 1962. The distribution of feeding habits among animals in a tropical rain forest. *Journal of Animal Ecology*, **31**(1): 53-63.
- Henderson, P. A. & R. M. H. Seaby, 1998. *Species diversity and richness 2.3*. Pisces Conservation Ltd.
- Hoch, G. A. & G. H. Adler, 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechymis semispinosus*). *Journal of Tropical Ecology*, **13**(1): 51-58.
- Jansen, P. A. & P. M. Forget, 2001. Scatterhoarding rodents and tree regeneration. In: Bongers, F., P. Charles-Dominique & P. M. Forget (eds.), *Dynamics and plant-animal interactions in a neotropical rainforest*. Kluwer Academic Publishers, The Netherlands. Pp. 275-288.
- Janson, C. H. & L. H. Emmons, 1990. Ecological structure of the non-flying mammal community at Cocha Cashu biological station, Manu National Park, Peru. In: Gentry, A. H. (ed.) *Four Neotropical Rainforests*. Yale University Press, New Haven. Pp. 314-338.
- Janzen, D. H., 1971. Seed predation by animals. *Annual Review of Ecology and Systematics*, **2**: 465-492.
- Janzen, D. H., 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica*, **6**(2): 69-103.
- Kelly, D., 1994. The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, **9**(12): 465-470.
- Kelly, D. & V. L. Sork, 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, **33**: 427-447.
- Leighton, M. & D. R. Leighton, 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton, S. L., T. C. Whitmore & A. C. Chadwick (eds.), *Tropical Rain Forest: Ecology and Management*. Blackwell Science, Oxford, UK. Pp. 181-196.
- MacArthur, R. H. & E. R. Pianka, 1966. On optimal use of a patchy environment. *American Naturalist*, **100**(916): 603-609.
- Marsh, C. W. & A. G. Greer, 1992. Forest-land use in Sabah, Malaysia: an introduction to Danum Valley. *Philosophical Transactions: Biological Sciences*, **335**(1275): 331-339.
- Newberry, D. M., E. J. F. Campbell, Y. F. Lee, C. E. Ridsdale & M. J. Still, 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia - structure, relative abundance and family composition. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **335**(1275): 341-356.
- Ng, F. S. P., 1991. *Manual of Forest Fruits, Seeds and Seedlings. Volume 1*. Forest Record No. 34. Forest Research Institute of Malaysia (FRIM). 400 pp.
- Sakai, S., 2002. General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biological Journal of the Linnean Society*, **75**(2): 233-247.
- Sakai, S., K. Momose, T. Yumoto, T. Nagamitsu, H. Nagamasu, A. A. Hamid & T. Nakashizuka, 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany*, **86**(10): 1414-1436.
- Schnurr, J. L., R. S. Ostfeld & C. D. Canham, 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. *Oikos*, **96**(3): 402-410.
- Smythe, N., 1986. Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals. *Annual Review of Ecology and Systematics*, **17**: 169-188.
- Sodhi, N. S., K. S. H. Peh, T. M. Lee, I. M. Turner, H. T. W. Tan, D. M. Prawiradilaga & Darjono, 2003. Artificial nest and seed predation experiments on tropical southeast Asian islands. *Biodiversity & Conservation*, **12**: 2415-2433.
- Terborgh, J., 1986. Community aspects of frugivory in tropical forests. In: Estrada, A. & T. H. Fleming (eds.), *Frugivores and seed dispersal*. W. Junk, Dordrecht, The Netherlands. Pp. 371-384.
- Wells, K., M. Pfeiffer, M. B. Lakim & K. E. Linsenmair, 2004. Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia. *Journal of Biogeography*, **31**(4): 641-652.
- Wolff, J. O., 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy*, **77**(3): 850-856.
- Wong, T. C. M., N. S. Sodhi & I. M. Turner, 1998. Artificial nest and seed predation experiments in tropical lowland rainforest remnants of Singapore. *Biological Conservation*, **85**: 97-104.
- Wright, S. J., H. Zeballos, I. Dominguez, M. M. Gallardo, M. C. Moreno & R. Ibanez, 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology*, **14**(1): 227-239.
- Wyatt, J. L. & M. R. Silman, 2004. Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. *Oecologia*, **140**(1): 26-35.