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NOTE

EVIDENCE FOR SCATTER-HOARDING IN A TROPICAL PEAT SWAMP FOREST IN MALAYSIA

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Many seed eating mammal and bird species cope with seasonal food shortage by hoarding seeds. Some hoarding species act as dispersers because they bury seeds in spatially scattered caches with few seeds each, a proportion of which is never recovered, allowing seedlings to establish. Large-seeded tree species may depend entirely on this 'scatter-hoarding' for recruitment (Vander Wall 1990). Scatter-hoarding by forest animals has been extensively documented in Europe and the Americas (e.g. Forget 1991, Forget *et al.* 2002, Vander Wall 1990), and to a lesser extent in Australia (e.g. Dennis 2003, Theimer 2001, 2003, Murphy *et al.* 2005), but hardly in Africa and Asia (Corlett 1998, Forget & Wenny 2005, Midgley *et al.* 2002). It has scarcely been studied in the Malay Archipelago: we found only one study reporting that a small proportion (less than 2%) of the experimental dipterocarp seeds were cached in a dipterocarp forest in Sabah (Maycock *et al.* 2005). Moreover, records of scatter-hoarding are lacking for tropical peat swamp forests, which cover some 38 Mha globally (Rieley *et al.* 1996), and which are an especially common ~~al~~though rapidly disappearing ~~fo~~rest type in the Malay Archipelago. Intuitively, scatter-hoarding seeds in soils that are seasonally flooded does not appear an adequate strategy to mitigate conditional food shortage, yet whether and how animals store seeds in these habitats has never been studied. Here we present results from a study on seed removal and post-removal seed fate in a tropical peat swamp forest in Borneo, specifically in Sarawak, Malaysia. The main aim of the study was to determine whether scatter-hoarding occurred in these seasonally flooded forests.

The research was done in a coastal peat swamp forest in Sarawak. The study site was located in the mixed swamp forest zone which is typically occurring on the outer ring of peat domes where ramin (*Gonystylus bancanus*) is one of the dominant tree species (Anderson 1961, Bruenig 1990). The forest is seasonally flooded, except for small bog mounds around many but not all trees. Sarawak peat swamp forests have seasonal fruiting (L. A. Dibor, personal observation), so animals face predictable annual periods of relative food shortage that could induce seed hoarding (Forget *et al.* 2002). If any seeds were scatter-hoarded in soils of these forests, the bog mounds seem the best locations because the stored food will remain accessible even during floods.

We conducted field work in June 2004 during the dry season (May–August) when the forest was not flooded. Our study site is a protected water catchment area (483 ha) covered by relatively undisturbed peat swamp forest near Lingga (1° 21' N, 111° 10' E), central Sarawak. We established 12 seed stations, each containing 25 fresh seeds of non-native jackfruit (*Artocarpus heterophyllus,* Moraceae). *Artocarpus heterophyllus* seeds were used because seeds of native peat swamp forest plants in the research area were not available, and they seem a reasonable model for large seeds in the region (Sodhi *et al.* 2003).

Seeds (~ 30 mm long) weighed between 3.1 and 10.8 g and were easily noticed on the forest floor because of their white-yellow colour. They were arranged in a 5 × 5 m grid with 25 cm interspacing, allowing animals to move between the seeds. We situated the stations below the most

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abundantly fruiting trees or lianas in the study area, i.e. locations that we expected to attract animals. The distance between seed stations was at least 20 m. All seeds were individually thread-marked with one meter of green coloured fishing line (diameter 0.4 mm) attached to the seed through a small drilled hole (see Forget 1990). A numbered 5 cm piece of pink-fluorescent flagging tape was glued to the distal end of the thread. Thread marks facilitate the retrieval of removed seeds because the mark usually remains visible even when seeds are eaten or buried (Forget 1990).

Five seed stations (stations 1 to 5) were established with seeds of ~ 25 mm length and a mean weight of 5 g (range between 3.1 and 7.3 g). Seeds were randomly distributed over the stations on 11 June 2004. One week later another five seed stations (stations 6 to 10) with fresh and bigger seeds of ~ 40 mm length and a mean weight of 8.3 g (range between 4.3 and 10.8 g) were installed. Two seed stations which were completely depleted (station 5 after 10 days and station 7 after one day) were replaced by two new seed stations (stations 11 and 12) on the same spots. These stations were also completely depleted within two days. Seeds offered in the first week (stations 1 to 5) were significantly lighter and smaller than seeds offered one week later (stations 6 to 12) (ANOVA: $F_{1,298} = 747.8$, $p < 0.001$ (seed mass); $F_{1,298} = 125853.9$, $p < 0.001$ (seed length)).

Stations were checked daily for three weeks (unless depleted earlier), and the time and order of seed handling by animals were recorded. Removed seeds were retrieved by searching the surrounding area in a 20 m radius assuming that rodents usually do not carry seeds for longer distances. Buried seeds were revealed by thread marks protruding from the soil. Five seed fates were distinguished: (1) not removed and intact, (2) eaten at seed station, (3) eaten away from seed station, (4) removed and cached, and (5) removed but not located. For hoarded seeds, we measured distance and direction of dispersal from the centre of the seed station, as well as the height above the ground level. We monitored bait stations with video cameras (Jansen & Den Ouden 2005) to identify the animals responsible for seed predation and seed dispersal at four of the seed stations. The video equipment consisted of a digital camcorder (Sony DCR-TRV14E) in a weatherproof housing (Sony SPK-TRV33), triggered by a passive infrared sensor (TrailMaster TM400v). The sensor detects movements of warm-blooded animals in a 150° wide and 4° high area of sensitivity. An external infrared lamp (Vision HP98IR; 940 nm*20) was used for night recording. Video recording was successful during the first 10 days only. On the other hand the registration of visits by the infrared sensor was successful during the whole three-week period. The other eight stations were not monitored by video.

The sensor recorded 57 visits at the four stations. Most events (72%) occurred between midnight and dawn. Murids, probably whitehead's rat (*Maxomys whiteheadi*) or Muller's rat (*Sundamys muelleri*), were identified eight times from the video recordings as nocturnal seed removers (Payne & Francis 1998). Diurnal visitation (25%) was mostly by squirrels, probably plantain squirrel (*Callosciurus notatus*). In most cases, subsequent visits were shortly after each other, suggesting that the same individual visited the seed station repeatedly. Three weeks after station establishment, 191 (63.7%) of the 300 experimental seeds had been handled and of these 185 (61.7% of total) were removed from the station (Table 1). We located 19 of the removed seeds: 10 seeds were eaten away from the station and 9 seeds were cached. We found four of the cached seeds in four different tree cavities at about 1 m above the ground. We assume that these seeds were hoarded by murids because the cavities were too small for squirrels to enter. We found the other five seeds between tree roots on bog mounds ranging in height between 20 and 50 cm. Most (166) out of the 185 removed seeds were not located, or only their marker was found, so their seed fate remains unknown. The mean dispersal distance of the cached seeds was 6.0 m (± 5.3 m). Seed removal was significantly faster for seed stations 6 to 12 (3.0 ± 0.1 days) than for stations 1 to 5 (8.2 ± 0.2 days) (log rank test: $\chi^2 = 116.0$, df = 1, $p < 0.001$). The remaining 109 seeds (36%) had not been handled after three weeks. Most (74%) of these were in the first series of stations (smaller size seeds). Non-removed seeds were significantly smaller than removed seeds in the second series of stations (ANOVA: $F_{1,173} = 8.04$, $p = 0.006$), but not in the first ($F_{1,123} = 0.03$, $p = 0.954$). There was no effect of seed mass on the rate of seed removal within stations (Cox regression with stations as strata: $Wald_1 = 0.004$,

Table 1 Fate of 300 thread-marked jackfruit seeds placed in peat swamp forest at Lingga, Central Sarawak

	Seed fate					
	Not handled	Handled				Total
		Not removed	Removed			
		Eaten at station	Eaten away from station	Cached	Not located	
Total count	109	6	10	9	166	300
% of total	36.3%	2.0%	3.3%	3.0%	55.3%	100.0%

Seed fate was monitored for three weeks during June 2004

p = 0.95) or within the two groups of stations (groups as strata: $Wald_1 = 2.45$, p = 0.12).

Our study is the first to report scatter-hoarding from seasonally flooded peat swamp forest, where scatter-hoarding in soil may not a priori seem an adaptive strategy. The rodents cached seeds at elevated locations (both bogs and tree cavities) which are rarely flooded and will hence be accessible at any time. Peat swamp forest trees grow best on naturally occurring mounds which suggests that cache site selection may favour seedling establishment and growth (Nuyim 2000). This was, however, not investigated in this study.

Our study is the second that reports scatter-hoarding for the Malay Archipelago. Maycock *et al.* (2005) found evidence of scatter-hoarding in a dipterocarp forest in Sabah where a small proportion (less than 2%) of the experimental dipterocarp seeds were cached. The existence of scatter-hoarding in Borneo is not surprising given its occurrence in the region like, for instance, Peninsular Malaysia (Yasuda *et al.* 2000). The occurrence of scatter-hoarding in the Malay Archipelago is especially interesting given the abundance of large-seeded tree species such as Dipterocarpaceae and Fagaceae. Ashton (1988) mentions the possibility of rats hoarding dipterocarp seeds in Borneo forests, and Yasuda *et al.* (2000) showed experimentally that dipterocarp seeds were scatter-hoarded by rodents at Peninsular Malaysia. The potential dispersal function of these animals is, however, not generally acknowledged (see Curran & Leighton 2000, Curran & Webb 2000). Mast seeding has been shown to satiate rodents as seed predators and stimulate them to scatter-hoard and thus disperse seeds (e.g. Vander Wall 2002, Jansen *et al.* 2004), but whether this explanation also applies to the Dipterocarpaceae and their mast seeding remains unconfirmed (Maycock *et al.* 2005). This study used a small number of seeds of a non-native species. The field experiment was carried out during the dry season which may be a period of low fruit availability (although this needs to be confirmed for this forest type), causing rodents to immediately consume rather than hoard seeds (Forget *et al.* 2002). Additional experiments are needed during other periods (e.g. wet season with higher fruit availability) using large-seeded native species to verify whether scatter-hoarding is an important process in the regeneration ecology of peat swamp forests.

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