Seed Dispersal by Mammals in Different Harvesting Intensities with Reduced-Impact and Conventional Logging in Sabah, Malaysia

Yoshihiro Nakashima[1, 2], Hisashi Matsubayashi[1, 3]
[1]*Center for Ecological Research, Kyoto University*
[2]*Present, Laboratory of Human Evolution Studies, Kyoto University*
[3]Present,Tokyo University of Agriculture

Introduction

Large mammals and birds are highly vulnerable to human disturbance such as hunting, habitat fragmentation and forest logging (Peres 2000), and their populations have rapidly diminished especially in Southeast Asia (Corlett 2002). Recent studies of fruit–frugivore interactions showed that large-seeded plants depend on large frugivores for seed dispersal (Corlett 1998; Kitamura et al. 2002). Large-seeded plants may thus be negatively affected by the decline of such animal populations. Urgent research is required into interactions between large-seeded fruits and frugivores where the latter still occur (Kitamura et al. 2002).

Reduced-impact logging is a set of guidelines to reduce the physical impacts on the ground, remaining standing trees, streams and ecosystem as a whole with the combination of a pre-harvest census, carefully controlled felling and skidding, lowered allowable cut and regulated machinery use (Putz and Pinard 1993). Previous studies showed that relative densities of frugivorous mammals such as orangutan and civets (Viverridae) were higher in reduced-impact logged forest than in conventional logged forest in Sabah, Malaysia (Ancrenaz et al. 2005; Onoguchi 2007). As a next research question, we need to know if and how the difference in the density of frugivorous mammals translates to seed dispersal.

To understand the fruit-frugivore interaction in different harvesting intensities between reduced-impact and conventional logging, we investigated the seed dispersal by mammals in both forests. We conducted (1) the identification of seed dispersers of genus *Durio* that is one of the largest-seeded groups in Southeast Asia, with direct observation and camera trap, and (2) the comparative study on seed dispersal by civets that is one of the most important seed dispersers in Southeast Asia with route census in reduced-impact logged forest and conventional logged forest.

Materials & Methods

Study site

Our study was conducted in Deramakot Forest Reserve (55,083ha), a reduced-impact logged forest and adjacent Tangkulap Forest Reserve (27,550ha), a conventionally logged forest, in Sabah, Malaysia. The climate is humid equatorial with a mean annual temperature of about 26℃. Mean annual rainfall is about 3,500 mm (Huth and Ditzer 2001). The major vegetation of Deramakot is a mixed dipterocarp forest dominated by the family Dipterocarpaceae, while that of Tangkulap is a forest dominated by pioneer species such as the genus *Macaranga* (Euphorbiaceae) (Seino et al. 2006). All of the large mammal species of

Sabah, including Asia elephants *Elephas maximus* (Linnaeus, 1758), orangutans *Pongo pygmaeus* (Hoppius, 1763) and sun bears *Helarctos malayanus* (Raffles, 1821), with the exception of the Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814), inhabit these forests (Matsubayashi et al. 2006; Onoguchi 2007; Matsubayashi et al. in press).

Focal Durio species

The studied durian species were *Durio graveolens* Becc. and *D. zibethinus* Murray. Both species have the typical fruit structure of *Durio*, with large, tough husks and acute spines, containing arillate seeds, but the species vary in aril color, and the timing of dehiscence. *Durio graveolens* has a pale orange globose husk, 10.1 ± 1.4 cm long and 9.1 ± 1.2 cm wide (mean ± SD, n = 20), which completely splits into five valves on the tree (before the fruits fall). The seeds, 3.8 ± 0.5 cm long and 2.0 ± 0.1 cm wide (n = 30), are surrounded by red aril which is not sweet and has no odor. The number of seeds per fruit is 7.6 ± 2.2 (n = 20). In contrast, *D. zibethinus* has an ellipsoid green husk, 13.2 ± 3.1 cm long and 10.0 ± 3.3 cm wide (n = 20), which opens after the fruits have fallen. The seeds, 3.9 ± 0.3 cm long and 2.6 ± 0.2 cm wide (n = 30), are surrounded by white aril which is sweet in taste with a strong odor. The number of seeds per fruit is 5.5 ± 3.2 (n = 20).

Study sites are *ca* 30 km from the nearest village, and no fruits were removed by humans. In 2005, *Durio* bore many fruits from July to September in Deramakot. Observations were conducted at three *D. graveolens* trees (tree code: ET1, ET2, and ST3) and one *D. zibethinus* (K5). The *D. graveolens* trees were 223 ± 46 cm dbh, while the *D. zibethinus* was 345 cm. Our observations started before fruits were fully matured (developed full in fruit size with incomplete arillate seeds).

Camera trap and direct observation

When fruits were still immature (*i.e.*, intact on the trees for both species), both durian species were watched from a concealed position on the ground *ca* 20 m from the tree from 0530 h to 1830 h in almost all weather conditions except heavy rain (ET1: 28 July–7 August, ET2: 11–17 August, ST3: 5–12 September, K5: 3–16 August). When fruits matured (*i.e.*, those of *D. graveolens* retained on the tree, but those of *D. zibethinus* fallen), *D. graveolens* trees were observed directly from 0530 h to 0030 h (ET1: 8–10 August, ET2: 18–20 August, ST3: 13–19 September), and *D. zibethinus* was monitored with an automatic digital camera system (CAMEDIA digital camera X-350, OLYMPUS, and Magical Finger HAS-NF1, HOGA, Japan) on a 24-h basis (K5: 15–31 August). For the latter, we relocated all dropped fruits of *D. zibethinus* to the front of the automatic camera system.

In direct observation, we recorded the following: (1) visiting animal species; (2) length of time on tree; (3) the number of fruits consumed; and (4) the method of handling the seeds. We were unable to precisely count the number of fruits consumed, since fruits were concealed by leaves. Thus, the number of fruits consumed by each individual was estimated based on the number consumed during direct sightings divided by the proportion of the duration of direct sighting to the total duration of the visit. These points could be materialized for both species in most cases. Even when using an automatic camera, (3) and (4) were recorded by applying no photographic delay interval, which enabled us to use the camera like a video camera. Total fruit number was estimated from the total number of fallen husks with intact stalks during one season. This is likely to be an underestimate, because we may have overlooked fallen husks with intact stalks, and we observed that some animals consumed fruits after removal beyond the crown of a mother tree, so total fruit number here is approximate one. These observations were continued daily until all fruits which could be seen from the ground had been consumed. In total, we conducted 288 h direct observation on *D. graveolens* (ET1: 93 h, ET2: 65 h, ST3: 130 h), and 96 h direct observation and 384 h observation with the automatic camera on *D. zibethinus* (K5: 504 h).

Route census of seed dispersal

We conducted route census with a total of 30 km logging road, 17km in the reduced-impact logged forest for 52 days and 13km in the conventional logged forest for 23 days in 2004 and 2005 on foot and by motorbike during day. Dispersed seeds with feces of civets were photographed (Fig. 1), and the seeds were classified by aril color and shape. To identify seeds, we relied on Jaiwit P. and Gubilil M. who are the staff of Forest Research Centre, Sabah Forestry Department. We compared the frequency of the detection of the feces and number of the seeds species recorded in both of the forests.

Results

Seed dispersers of the Durio

Total fruit number was 99, 27, 252 and 58 at ET1, ET2, ST3 and K5, respectively. The results of our observations are shown in Table 1. We defined dispersal (D) as transporting seeds 20 m or more from the parent tree, neutral consumption (NC) as dropping intact seeds under the parent tree crown and predation (P) as destroying seeds.

During our observations of both species, orangutans consumed more fruits than any other consumers (ET1: χ^2 = 46.1, df = 1, P < 0.001; ET2: χ^2 = 21.2, df = 1, P < 0.001; ST3: χ^2 = 162, df = 1, P < 0.001; K5: χ^2 = 29, df = 1, P < 0.001; Table 1). When orangutans visited the trees, arillate seeds were still immature. They plucked fruits with hands and/or teeth, and easily tore apart husks with their hands and incisors. They picked up the arillate seeds, sucked aril, chewed the seed and spat out only the seed coats. At times, they made longer visits, making a bed on or near a fruiting tree and consuming fruits on two consecutive days. One male consumed 119 fruits during two days in one visit. In terms of function, they therefore appear to be the most important predators.

When *D. graveolens* matured, fruits dehisced on the trees, and they were consumed mainly by arboreal animals; Prevost's squirrels *Callosciurus prevostii* (Desmarest, 1822), black hornbills *Anthracoceros malayanus* (Raffles, 1822), civets (Viverridae) and long-tailed macaques *Macaca fascicularis* (Raffles, 1821)(Table1). Black hornbills visited two trees (ET1, ST3), swallowed arillate seeds and did not regurgitate before leaving the tree, so they clearly dispersed seeds. The number of seeds handled by them (Table 1) was probably overestimated, especially at ST3, because they did not appear to eat fruits when perched in places that we were unable to observe. We directly observed hornbills eating only 7 seeds in 4 fruits. A civet visited one tree (ET1) during the night. The animal was concealed by leaves, so we were unable to identify it to species or how it handled the seeds. However, when we fed three captive common palm civets *Paradoxurus hermaphroditus* (Pallas, 1777) with *D. graveolens* fruits, they chewed and destroyed the seeds, and swallowed them (Y. Nakashima pers. obs.). In summary, *D. graveolens* seeds were predated mainly by orangutans and dispersed by black hornbills.

In contrast, *D. zibethinus* fruits were consumed once fallen to the ground, mainly by terrestrial animals (Table 1). Fruits remained unopened on the ground for some time. Before the fruits opened naturally, sun bears *Helarctos malayanus* visited and opened them with their clacks or teeth. The bears ate only arils and spat out intact seeds, so they are neutral consumers in our observations. Long-tailed giant rat *Leopoldamys sabanus* (Thomas, 1887), large tree shrew *Tupaia tana* (Raffles, 1821), horse-tailed squirrel *Sundasciurus hippurus* (Geoffroy, 1831), Malayan porcupine *Hystrix brachyura* (Linnaeus, 1758) and long-tailed porcupine *Trichys fasciculata* (Shaw, 1801) were observed to visit the seeds left by the sun bears. Long-tailed giant rats sometimes carried seeds in their mouths and these seeds were probably quickly predated. When we traced 200 seeds of *D. zibethinus* (and 100 *D. graveolens*) with a thread-marking method (Yasuda et al. 2000), most seeds were predated within 1 day, and we have no evidence that scatter-hoarded seeds grew to seedlings (Y. Nakashima, unpublished data). Long-tailed macaques visited when the fruits were already dehisced on the ground. They cleaned arils in front of the mouth and then dropped the seeds. They sometimes carried the fruits > 10 m by hand. We found seed and husk discarded 23 m from the mother tree (transporting the fruit the first 18 m). Thus, these macaques do transport seeds beyond the crown of a mother tree although this behavior may be rare. The *D. zibethinus* seeds were mainly predated by orangutans and dispersed by long-tailed macaques.

Seed dispersal by civets

Frequency of detection of the feces was greater in the reduced-impact logged forest (1.13feces/day; the total number of feces is 59; total census day is 52 days) than that of in the conventionally-logged forest (0.61feces/day; 14 feces and 23days). Table 2 shows the family of seeds and the probably number of species in each family. In total, 28 species of seeds were detected in two forests. Twenty-seven species were in reduced-impact logged forest, and nine species were in conventionally-logged forest. Eight of the nine species found in the conventionally-logged forest were also detected in the reduced-impact logged forest.

Discussion

Our results show that many fruits of the two durian (*Durio*) species are predated, especially by orangutans. The majority of seeds did not germinate due to high predation pressure by orangutans, despite high investment into extremely large fruits. Some studies reported that orangutans especially preferred the fruits of *Durio* (Rijksen 1978; Galdikas 1982, 1988; Leighton 1993). In areas inhabited by orangutans, *Durio* dispersal success is probably lower than that in uninhabited areas. Although we report a predominant role of orangutans as predators, we also observed them to discard > 1000 mature intact seeds under one *D. graveolens* tree (TL1). This suggests that seed handling strategy varies among individuals, or even between trees by the same individuals. Galdikas (1982) highlighted their role as dispersal agents after observing orangutans discard *D. oxleyanus* seeds up to 50 m away from a mother tree. However, at least in

Deramakot, this is unlikely to occur. We also found many discarded seed coats under the other 8 fruiting trees, suggesting that they usually destroy and eat seeds. We always found their beds on or near fruiting trees, indicating that they stayed for up to several days to consume fruits and did not transport the seeds beyond the crown of mother tree even when they spat out the seeds.

Ridley (1984) suggested that *Durio* species with small red arils are probably dispersed by hornbills, and *D. zibethinus* is dispersed by bears. Our observations support the former, but not the latter. When we fed two captive bears with *D. zibethinus* fruits at the Sepilok Orangutan Rehabilitation Centre in Sabah, they did not swallow seeds. However, one individual at Sandakan Crocodile Farm in Sabah swallowed and excreted the intact *D. zibethinus* seeds. These results suggest that seed handling strategies differ among and/or within individuals of bear. In the wild, the Asian elephant *E. maximus* can probably also disperse seeds of *D. zibethinus*. The intact seeds were observed in their feces in the natural habitat. (A. Ahmad who is a staff of Sabah Forestry Department, pers. comm.). In addition, Prevost's squirrel may carry the seeds of the two species at least as far as to the adjacent tree crowns, as was reported in Peninsular Malaysia (Becker et al. 1985), although we did not observe such a behavior.

Our results suggest that both *Durio* species studied face difficulties with seed dispersal due to high predation pressure, especially by orangutans, and limited occurrence of alternative dispersal agents. The low density of wild *Durio* may be in part caused by high predation pressure. Our study did not reveal the main seed dispersers of *D. zibethinus*, but it is clear that the two *Durio* species are dispersed by different animals; *D. graveolens* by hornbills and *D. zibethinus* by large terrestrial mammals such as elephant and bear. These animals have been reported to be negatively affected by habitat degradation including fragmentation and logging (Corlett 2002). Therefore, our results suggest that the loss of large animals due to habitat degradation affects the regeneration of both species of *Durio*.

The frequency of the occurrence of civet feces and the number of dispersed seeds tended to diminish in the conventionally logged forest than in the reduced-impact logged forest. The former may reflects the reduction of the density of civets in the conventionally-logged forest. Seven species of civets were recorded in Deramakot (Matsubayashi et al. 2006; Onoguchi 2007; Matsubayashi et al. in press). Although we could not identify the species of civet for each dispersed seed, much of the seeds might have been dispersed by common palm civet *P. hermaphroditus* and/or Malay civet *Viverra tangalunga* (Gray, 1832) because these two species were often observed on the road at night and the density (indexed by camera trap) of those species tended to decrease in the conventionally-logged forest (Onoguchi 2007). The latter may reflect the decrease of the food resources for civets in the conventionally-logged forest. For example, seeds of Sapotaceae (Fig.1; vernacular name, Nyatoh), a group of climax trees that are commercially harvested, were detected in the reduced-impact logged forest only. The seeds of Sapotaceae could not be detected in the conventionally-logged forest probably because Sapotaceae tree were heavily harvested.

Our results correspond with the previous comparative study on vegetation and mammal fauna in the two forests (Seino et al. 2006; Onoguchi 2007), and imply that heavier logging intensities cause the degradation of the ecological function of civets, which in turn may feed-back to the forest regeneration through reduced seed dispersal.

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Table 1. The estimated numbers of the durian fruits consumed by each of visiting animals.

Tree species	Tree code	Animal species	Seed handling[1]	Unripe fruit Visits (*N*)	Unripe fruit Fruit consumed (*N*)	Ripe fruit Visits (*N*)	Ripe fruit Fruit consumed (*N*)
D. graveolens	ET1	*Pongo pygmaeus* (♀)	P	1	62	0	0
		Callosciurus prevostii	NC/P	3	0	4	3
		Macaca fascicularis (♂)	NC	0	0	1	3
		Viverridae sp.	-	0	0	1	?
	ET2	*P. pygmaeus* (♀)	P	1	24	0	0
		C. prevostii	NC/P	2	0	1	1
		Anthracoceros malayanus (♂)	D	0	0	1	0
	ST3	*P. pygmaeus* (♂)	P	2	206	0	0
		C. prevostii	NC/P	0	0	1	4
		A. malayanus (♂)	D	0	0	3	12
D. zibethinus	K5	*P. pygmaeus* (♀)	P	1	52	0	0
		C. prevostii	NC/P	2	1	0	0
		Helarctos malayanus	NC	0	0	7	16
		M. fascicularis (♂, ♀)	NC/D	0	0	1	9
		Leopoldamys sabanus	P	0	0	1	1

Tree codes correspond to main text.

[1]P = predation, NC = neutral consumption, D = dispersal

Table 2. Family of the seeds found in civet feces and the estimated number of species in each family in the reduced-impact logged forest and the conventionally-logged forest.

Census sites	Family	Detected no. of species (total)
Reduced-impact logged forest	Annonaceae	2
	Cucurbitaceae	1
	Leeaceae	1
	Meliaceae	3
	Passifloraceae	1
	Sapotaceae	1
	Solanaceae	1
	Theaceae	1
	Unidentified	16
		(27)
	Meliaceae	1
	Passifloraceae	1
Conventionally-logged forest	Rubiaceae	1
	Unidentified	6
		(9)

Figure 1. Dispersed seeds (Sapotaceae) in the feces of civets in the reduced-impact logged forest.