

A Preliminary assessment of seed dispersal by two ape species in the Sabangau,
Indonesian Borneo

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Abstract

A preliminary assessment of seed dispersal by the Bornean agile gibbon *Hylobates albibarbis* and the Bornean orang-utan *Pongo pygmaeus wurmbii* was carried out in the Sabangau catchment, Borneo. Defecations were analyzed to determine the number and species of seed they contained. Defecated seeds were then planted and monitored for germination; where possible controls were collected for comparison. *Ficus* seeds were the only seeds found in sufficient abundance to test the effect on germination of planting condition (*peat, faeces* or *petri*). Seedlings were planted and monitored for three weeks to assess factors affecting young seedling growth.

1. 27 orang-utan defecations and 14 gibbon defecations were examined; 66.7% orang-utan defecations contained intact seeds while 100% of gibbon defecations contained intact seeds.

2. Gibbon defecations were significantly more species rich than orang-utan defecations ($p=0.000$) with means of 2.429 ± 0.40 and 0.742 ± 0.22 species of seed per defecation respectively.

3. Germination trials on identified non-*Ficus* defecated seeds showed that four of eight species defecated by gibbons germinated, while zero of two orang-utan defecated species germinated. Controls collected for two species did not show a significantly different germination success.

4. Germination success was extremely low for *Ficus* seeds and statistically similar for seeds planted under different conditions (*faeces, peat, petri*). In addition, there was no difference in germination success between control, orang-utan defecated and gibbon defecated seeds.

5. Growth analysis was limited, however mortality was much higher for the small seeded *Ficus* seedlings than the larger seeded seedlings.

1. Introduction

In the plant kingdom, there is a huge diversity of seed dispersal mechanisms, from those which are wind and water dispersed, to those which are animal dispersed and often surrounded by a rewarding fleshy fruit. Several theories have been proposed to try to explain the phenomenon of seed dispersal. First, the 'escape hypothesis' (Janzen 1970, Howe and Smallwood 1982) states that seeds dispersed away from the parent plant have an increased chance of survival due to reduced sibling and parent competition. In addition, seeds or seedlings clumped together are more likely to be found and hence destroyed by pathogens and predators. Much subsequent research has shown disproportionate mortality near the parent tree to be the case for many plants (e.g. Clark and Clark 1984, Howe 1986). Second the 'colonization hypothesis' (Howe and Smallwood 1982), proposes that due to habitat variability, a parent plant can spread the risk of seed and seedling mortality by dispersing propagules widely. In this way, although many will be dispersed to sub-optimal habitats, a few are likely to colonize new areas and optimal sites. Third, the 'directed dispersal' hypothesis (Howe and Smallwood 1982), although originally thought unlikely to be of much significance in many cases of vertebrate dispersed plants (Wheelwright and Orians 1982), is now thought to be of some importance (Wenny 2001). This hypothesis states that the dispersal mechanism employed by the parent plant can direct seeds to optimal microhabitats suitable for seed germination and subsequent growth. Since the original seed dispersal theory has been published, a considerable amount of work in the field has been carried out, especially for the significance of vertebrates such as primates in the dispersal of seeds (reviews: Chapman & Onderdonk 1997, Corlett 1998).

The interaction between vertebrate disperser and plant is an interesting one; while the animal usually gains valuable food, often in the form of a carbohydrate rich fruit pulp, the parent plant is able to disperse its seeds via the animal. Such interactions have only very rarely been seen between solely two species; two notable examples of this being of the gorilla, *Gorilla gorilla* and *Cola lizae* seeds (Tutin *et al.* 1991) and the dodo, *Raphus cucullatus*, and *Calvaria major* seeds (Temple 1977). Usually, plant seeds are dispersed by a whole host of vertebrate frugivores, while these frugivores themselves rely on more than one species for food. The quality of a vertebrate frugivore as a seed disperser can vary greatly; some kill seeds when consuming fruit while others may disperse large numbers of intact seeds. In general, a high quality seed disperser will not damage the seeds which it handles, and will either defecate or spit such seeds in high quantities in sites suitable for seedling establishment and growth (Schupp 1993).

Primates in particular have long been thought to play an important role in seed dispersal, due to the high fruit content in their diet, the often considerable distances they travel and their size; in tropical forests primates constitute between 25-40% of the total frugivore biomass (Eisenberg and Thorington 1973). Seed dispersal studies have been carried out for all great ape species (gorillas, Tutin *et al.* 1991; bonobos, Idani 1986; chimpanzees, Takasaki 1983; orang-utans, Galdikas 1982) and for many other primates (for example, gibbons, McConkey 2000; 2005; tamarins, Knogge *et al.* 2003; spider monkeys, cebus monkeys and howler monkeys, Chapman 1989). The methods used, and the specific aspects of seed dispersal studied vary hugely between these studies. For example, some studies only examined which species were present in the defecations of individuals (Galdikas 1982), while others carried out germination trials on the seeds

which they found (McConkey 2000, Knogge *et al.* 2003, Chapman 1989, Tutin *et al.* 1991, Idani 1986, Takasaki 1983). Some studies went further, and tried to examine seed and seedling fates *in situ* (Chapman 1989, McConkey 2000; 2005, Tutin *et al.* 1991). Results from investigations into the effect of gut passage on germination vary greatly even within disperser species studied. While the germination success and latency of some seed species are increased by ingestion and subsequent defecation, for example *Cola lizae* seeds defecated by gorillas (Tutin *et al.* 1991), gut passage seems to have an adverse affect on some species while having little or no effect on others (Review: Chapman and Onkerdonk 1997).

The importance of investigations involving the study of ecological interactions between species should not be underestimated, with many disperser and dispersed species currently on the brink of extinction; to quote Janzen 1974: “What escapes the eye ... is a much more insidious kind of extinction: the extinction of ecological interactions” (in: Bond 1994). The conservation of species such as the orang-utan and the gibbon and the habitat in which they live involves the understanding of how they interact with their environment. If such dynamic interactions are lost cascades of species may be affected; it has been proposed that primates are critical for forest regeneration (Chapman and Onderdonk 1988).

Primate seed dispersal had not been studied in the unique habitat of Indonesian tropical peat swamp forest prior to this investigation; in fact the tropical peat swamp forest ecosystem has received relatively little research attention until recently (Page *et al.* 1999). However, the Sabangau catchment in which the study took place contains one of the largest populations of the Bornean orang-utan *Pongo pygmaeus wurmbii* (Morrogh-

Bernard *et al.* 2003) and is the largest continuous area within the range of the Bornean agile gibbon *Hylobates albibarbis* (Cheyne *et al.* 2008). It is therefore of great importance that these populations be studied in order that their significance in the maintenance of this habitat is known, and so that comparisons can be made with other great ape populations in Indonesia.

Aims of the study

As primate seed dispersal had not been studied in this location before one of the main objectives of this study was the trialling of methods to facilitate possible future work. In addition, the main aims of the study included establishing which species of seed are dispersed by gibbons and orang-utans in this region, the numbers of such seeds in an average defecation, and whether the two ape species differ substantially as dispersers in this particular habitat. The aims also included the assessment of whether factors such as the presence of faeces affect germination; little work has previously been carried out on this. Species found in faeces in sufficient abundance were planted under three conditions. In addition, controls were collected from the forest, where possible, in order that the effect of gut passage on seed germination could be ascertained. Finally, the factors affecting growth of young seedlings were examined to see whether germination condition influences growth and mortality, again a novel experiment.

2. Materials and Methods

Data was collected at the natural laboratory for peat swamp forest (NLPSF), in the Sabangau catchment, Central Kalimantan, Indonesia (see fig. 1) from 27th June to 18th September which is during the dry season in this region. Seeds were germinated and seedlings grown in the Sabangau Seedling Nursery, which was purpose built inside the forest in order to house seedlings under natural conditions, while protecting them from predation (Graham *et al.* unpublished)

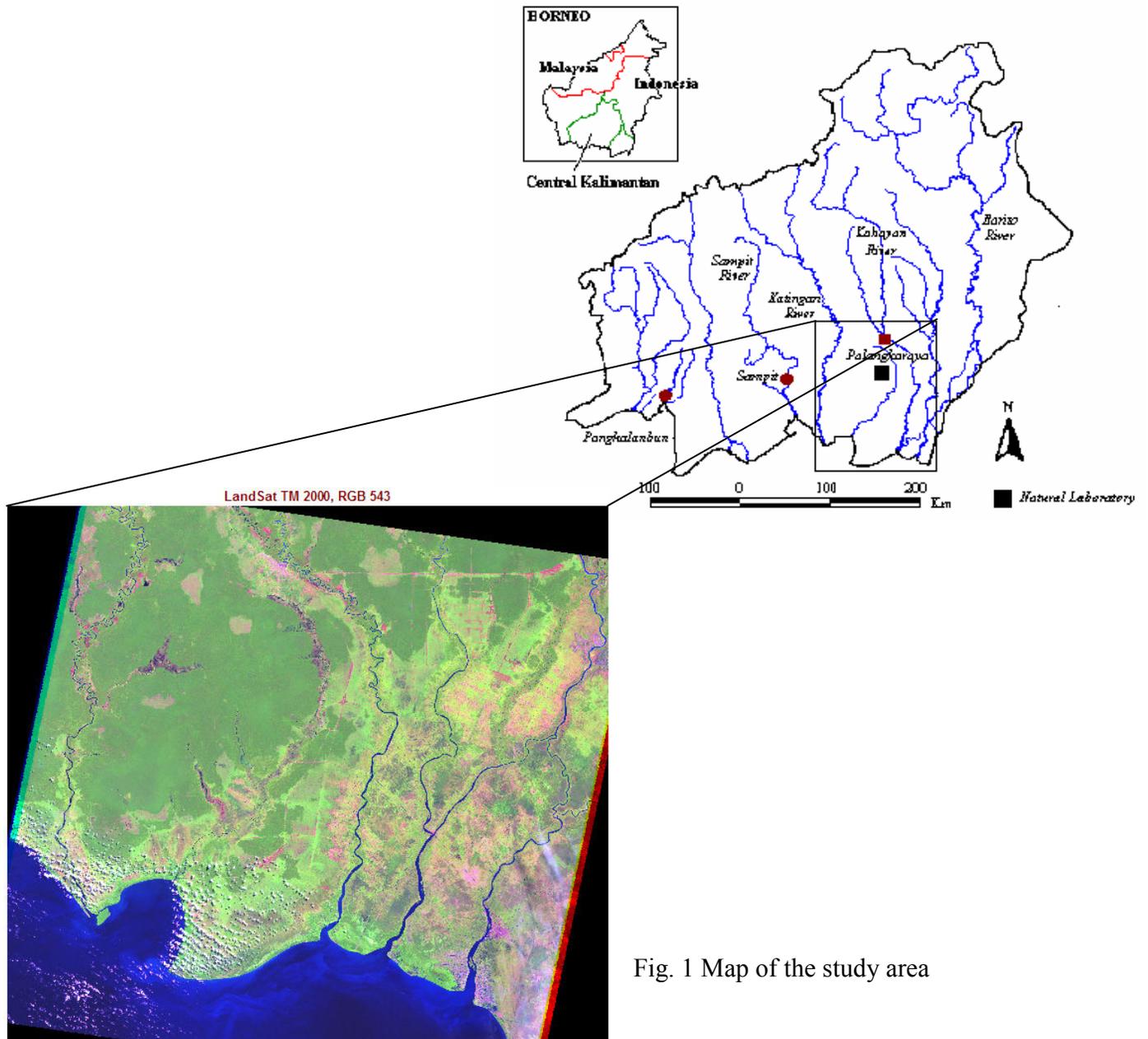


Fig. 1 Map of the study area

2.1 Defecation analysis:

Faeces were collected in the field by following individual orang-utans and by following gibbon groups, and collecting the faeces when it dropped from the animals in the canopy. The faeces were placed in plastic bags and transported back to camp where they were analyzed on either the same day or on the following day. Samples were weighed to an accuracy of 0.01g, and disseminated using forceps; the seeds were then extracted, identified and counted. Hereafter seeds will be divided into *Ficus* (Moraceae) and non-*Ficus* seed species; the distinction due to the fact that *Ficus* seeds were substantially smaller than any other identified seed and were found in much greater numbers than any other type of seed.

2.1.1 Non *Ficus* seed species:

Despite expert local knowledge, seed species identification still proved extremely difficult; seed identification is difficult even when the seeds have not previously passed through the gut of an ape. In some cases seeds of different species look similar, for example those from the genus *Syzygium* (Myrtaceae) and the genus *Zyzyphus* (Rhamnaceae); these could only be distinguished once the seeds had germinated. In addition, not all species could be identified to species level; some could be identified to genus level, while others not at all. Follow data from the relevant orang-utan or gibbon were used to try to identify unknown or uncertain seeds. However, in the case of gibbons these data would only be for the day the faeces was collected and not for when the fruit was actually eaten. Therefore while it gave some idea of which species were in fruit in the forest at any particular time, the data was not particularly useful. For orang-utans,

individuals were followed for up to 12 days and so a slightly longer term view of the diet of the individual could be ascertained.

2.1.2 *Ficus* species:

In this location ~9 species of fig have been identified. It was not possible to tell the species of *Ficus* seeds extracted from faeces as they are so small, and so the identification was to genus level only. In addition the small size of *Ficus* seeds meant counting the exact number per defecation proved difficult. The method was therefore amended once several defecations had already been analysed, so that the number of seeds in 4g of the defecation were counted and this could then be used to estimate the total number per defecation.

2.2 Planting the seeds:

Once seeds had been extracted, counted and identified they were then planted. For non-*Ficus* species, seeds could only be planted under one condition as there were only very few from each species found. For these seeds, a plate was prepared with sterilized peat collected locally and the faeces from which the seeds were extracted was then broken up and placed on top of the peat. The seeds were then placed on top of this and the plate watered regularly with rainwater.

For *Ficus* seeds, as such large numbers could be found in each defecation, it was possible to plant the seeds under different conditions to see how this affected percentage germination, germination delay and subsequent seedling growth. To begin with, seeds were planted in two different conditions: *faeces* and *peat*. The *faeces* condition was the

same as that described above for non-*Ficus* seeds. For the *peat* condition, the plate was prepared the same as for the *faeces* condition, but without adding the faeces; instead the seeds were placed directly on top of the peat, which was then watered. However germination success was so low in these two conditions for *Ficus* seeds that another germination medium was experimented with once the study was already underway; damp tissue paper on a petri dish. This has been used in previous studies into *Ficus* seed germination (McConkey 2000; Serio-Silva and Rico-Gray 2003; De Figueiredo 1993).

2.3. Germination of seeds:

Plates were labeled clearly and then placed in a seedling nursery under a tarpaulin. This was to prevent rain causing flooding of the plates and loss of seeds, as even in the dry season heavy downpours are common. The plates were checked daily for signs of germination. For the different species, slightly different measures of germination had to be used. *Ficus* seedlings were classed as ‘germinated’ when the dicotyledons could be seen as this was generally the first visible sign of germination, as the seedlings were so small and leaves were produced almost immediately. For other species, such as *Zyzyphus angustifolius*, protruding roots were the first visible sign of germination rather than shoots and hence leaves, and so therefore the seed was classed as ‘germinated’ when it was fully split open. Other species from genera such as *Syzygium* and *Willughbeia* (Apocyanaceae), produced shoots before roots, but leaves did not appear until much later (e.g. *Willughbeia* 18 days) and so seeds were also classed as germinated when fully split open rather than when a shoot could be seen.

2.4. Planting of germinated seeds:

Once germinated, seedlings were removed from the germination plates the same day and placed in individual poly bags filled with peat to eliminate sibling competition. It was decided not to transfer any of the original faeces across to the poly bags for several reasons. First, in the forest under more natural conditions, the faeces of an animal such as a gibbon or orang-utan is likely to be dispersed fairly rapidly. Therefore it is unlikely that by the time a seed is germinated there would be much faeces left; the fastest seed to germinate in this study was a *Ficus* seed which had a germination delay of 9 days. Second it would be difficult to standardize the quantity of faeces which should be transported with each seedling to the poly bags. In addition, with the *Ficus* seeds, as they are so tiny it would have been difficult to ensure that no non-germinated seeds were being transported alongside the seedlings to the poly bags.

2.5. Monitoring seedling growth:

Seedlings were monitored for 21 days; height was measured every 3 days from the day of planting, using a tape measure accurate to ± 0.1 cm. Seedling height here is defined as the length of the stem from the peat from which it is growing, to the apical meristem. For those species of seed where the seed itself remained attached (genera: *Willughbeia*, *Syzygium*, *Zyzyphus*), the length of the stem was measured from where it exited the seed to the apical meristem.

2.6 Light intensity

As the germination trays were all under the same tarpaulin in the nursery, it was assumed that light intensity was relatively constant. However, a slight difference was noticed in the 5th week of study and so light intensity was measured with a light intensity meter at three different positions along the germination bench. Light intensity was also measured at three positions along the bench where the seedlings were growing. Readings were taken every 30 minutes from 6.00 am to 5.00pm at each of the 6 positions.

2.7 Statistical analysis

All statistical analysis was carried out using Minitab 15.1.0.0 software, and graphs were created on Microsoft Office Excel 2003.

Proportion of gibbon and orangutan defecations containing intact and damaged seeds

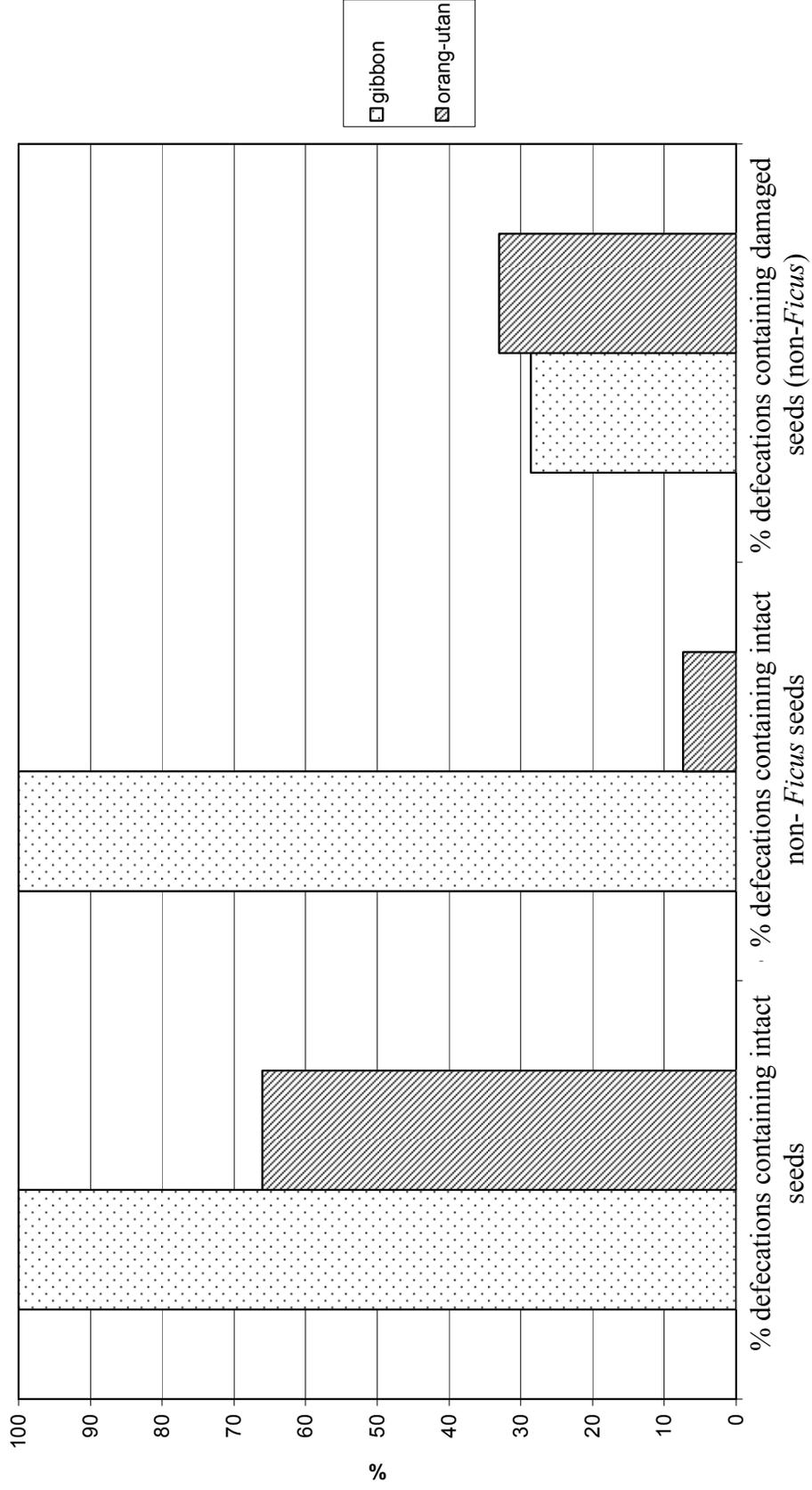


Fig 2. Chart to compare the proportion of gibbon and orang-utan defecations containing intact seeds (including those from the genus *Ficus*), intact non-*Ficus* seeds, and damaged seeds (all damaged seeds were non-*Ficus* seeds.)

Table 1 – Identified seeds in Gibbon defecations and their abundance:

Family	Species	mean no. intact seeds per defecation (N=14)	% defecations containing intact seeds of the species. (N=14)	Total no. of seeds from 14 defecations	No. of seeds in germination trial (post Damage+)	Germinated in 7 weeks?
Tetramenstaceae	<i>Tetramensta glabra</i>	0.29	21.40	4	3	No
Myrtaceae	<i>Syzygium</i> -	0.21-0.71*	7.10-28.6*	3-10*	3-4*	Yes
Apocynaceae	<i>Willughbeia</i> -	0.07	7.10	1	1	Yes
Anacardiaceae	<i>Camponosperma coriaceum</i>	0.07	7.10	1	1	No
Memspermaceae	<i>Fibraurea tinctoria</i>	1.07	35.70	15	11	Yes
Rhamnaceae	<i>Zyzyphus angustifolius</i>	0.29-0.79*	21.4-28.6*	5-11*	5-6*	Yes
Annonaceae	<i>Artobotrys</i> -	0.43	21.40	6	4	No
Sapotaceae	<i>Palaquium</i> -	0.14	7.10	2	2	No
Moraceae	<i>Ficus</i> -	604.00	100.00	8393	Seeds not predated	Yes

*Species *Syzygium* and *Zyzyphus angustifolius* could not be distinguished until after germination, and there was one seed which did not germinate; in addition these seeds were predated severely pre-germination, hence total number of seeds was not known exactly for either species.

+some seeds were destroyed in the nursery, possibly by rats (see discussion).

Table 2 – Identified seeds in orang-utan defecations and their abundance:

<i>Family</i>	<i>Species</i>	<i>Mean no. intact seeds per defecation (N=27)</i>	<i>% defecations containing intact seeds (N=27)</i>	<i>Total number of seeds in 27 defecations</i>	<i>Number of seeds in germination trial (post Damage+)</i>	<i>Germinated seeds in 7 weeks?</i>
Tetramenstaceae	<i>Tetramensta glabra</i>	0.04	3.70	1	1	No
Anacardiaceae	<i>Camponosperma squamatum</i>	0.04	3.70	1	0	-
Moraceae	<i>Ficus -</i>	177.10*	55.56	N/A	Seeds not predated	Yes

* *Ficus* seeds counted in a sample of 10 defecations

+ Some seeds were destroyed in the nursery, possibly by rats (see discussion)

Table 3 – Germination of non-*Ficus* seeds

<i>Family</i>	<i>Species</i>	<i>Proportion germinated control (%)</i>	<i>N</i>	<i>Proportion germinated defecated (within 7 weeks) (%)</i>	<i>N</i>	<i>P value (Fisher's exact test)</i>
Myrtaceae	<i>Syzygium</i> -	-	-	75.00-100.00	3-4	-
Apocynaceae	<i>Willughbeia</i> -	-	-	100.00	1	-
Memspermaceae	<i>Fibraurea tinctoria</i>	30	50*	9.10	11	0.259
Rhamnaceae	<i>Zyzyphus angustifolius</i>	-	-	83.30-100.00	5-6	-
Annonaceae	<i>Artobotrys</i> -	0	13**	0.00	4	1.000

* Monitored for 5 weeks

** Monitored for 7 weeks

Table showing those non-*Ficus* species which germinated (all from gibbon defecations) and those species for which control data could be collected (highlighted). The P value is for the difference in germination proportion between control and defecated seeds.

Table 9 - Comparing orang-utan, gibbon and control *Ficus* seed germination proportions

<i>Sample 1</i>	Mean germination proportion (%)	S.E.	<i>Sample 2</i>	Mean germination proportion (%)	S.E.	<i>P value</i>
Gibbon defecated seeds in <i>faeces</i> (N*=7)	1.79	0.89	Orang-utan defecated seeds in <i>faeces</i> (N=6)	2.71	0.62	0.222
Gibbon defecated seeds in <i>peat</i> (N=5)	2.74	1.29	Orang-utan defecated seeds in <i>peat</i> (N=5)	1.22	0.80	0.332
Orang-utan defecated seeds in <i>peat</i> (N=5)	1.22	0.80	Control seeds in <i>peat</i> (N=4)	0.25	0.25	0.561
Gibbon defecated seeds in <i>peat</i> (N=5)	2.74	1.29	Control seeds in <i>peat</i> (N=4)	0.25	0.25	0.073
Gibbon defecated seeds on <i>petri</i> (N= 8)	2.81	1.45	Control seeds on <i>petri</i> (N=4)	4.00	3.37	0.932

*N = number of defecations (batches for controls) seeds planted from; for each defecation/ batch at least 39 seeds were planted.

The germination proportions from gibbon defecations for each condition, orang-utan defecations and control seeds were compared using a Mann-Whitney U test. This made it possible to see if disperser species had an effect on *Ficus* seed germination success and whether gut passage had an effect on germination.

3. Results

3.1 Defecation analysis:

The aim of the defecation analysis was to determine the species of seed defecated by orang-utans and gibbons, the abundance of such seeds and the extent to which seeds are damaged. 14 gibbon defecations from 10 individuals and 27 orang-utan defecations from four individuals were analyzed over the period of study. 66.7% of orang-utan defecations contained intact seeds and 100% of gibbon defecations contained intact seeds. Damaged seeds were found in 28.6% of gibbon defecations, and 33% of orang-utan defecations. Gibbon defecations had a mean weight of 11.34g (S. E. = 2.02) while orang-utan defecations had a mean weight of 29.19g (S. E. = 3.22).

100% of gibbon defecations contained intact non-*Ficus* seeds with a mean of 4.14 (S. E. = 0.82) seeds per defecation, and 7.4% of orang-utan defecations contained intact non-*Ficus* seeds, with a mean of 0.07 (S. E. = 0.05) seeds per defecation (see fig.2) which is significantly different (Mann Whitney U test $p = 0.000$). Eight species in addition to those from the genus *Ficus* (Moraceae) were identified from gibbon defecations (see table 1) although *Syzygium* (Myrtaceae), *Artobotrys* (Annonaceae) and *Palaquium* (Sapotaceae) seeds were only identifiable to genus level (the seeds found for each genus appeared to be of the same species). Only two non-*Ficus* seeds which could be identified were found in orang-utan faeces (see table 2). Unfortunately it was not possible to identify all the non-*Ficus* seeds; there were 9 seeds from 6 Gibbon defecations which could not be identified, comprising an estimated 7 further species. In addition, seeds from the genus *Syzygium* and those of the species *Zyzyphus angustifolius* could not be distinguished until after germination; therefore the one seed which did not germinate, and

the seeds which were predated could not be identified. There were eight seed objects found in four orang-utan defecations which were assumed to be broken fragments due to their irregular shape but they could have been seeds of an unknown species; species, seed number, and broken seed data from orang-utan faeces could therefore be slight underestimates.

Seeds from the genus *Ficus* were by far the most abundant found in both gibbon and orang-utan faeces. 100% of gibbon defecations contained seeds from the genus *Ficus*, with a mean of 604 (S. E. = 257) seeds per defecation (seeds counted for 14 defecations) while *Ficus* seeds were found in 62.9% of orang-utan defecations. For those orang-utan defecations which contained *Ficus* seeds there was a mean of 177.1 (S. E. = 45.7) seeds per defecation (seeds counted for 10 defecations). The difference between gibbons and orang-utans in number of *Ficus* seeds per defecation (only including those defecations containing *Ficus* seeds) is not significant (Mann-Whitney U test $p = 0.3054$)

Orang-utan defecations had a mean species richness of 0.742 (S. E. = 0.11) species and gibbon defecations had a mean species richness of 2.429 (S. E. = 0.29) species. Gibbon defecations were significantly more seed species rich than orang-utan defecations (Mann-Whitney U test $p = 0.000$).

3.2 Germination analysis

By planting defecated seeds under different conditions and by comparing defecated seeds to control seeds, factors affecting germination could be elucidated.

3.2.1 *Non Ficus seeds:*

As only very low numbers of non-*Ficus* seeds were found in both orang-utan and gibbon defecations, the only effect which could be tested for these species was that of gut passage on germination and not that of germination condition. Of the eight non-*Ficus* species of seeds found in gibbon defecations, four species germinated within 7 weeks. However, for the remaining four species of which no seeds germinated, sample sizes were very low and so probably did not provide an accurate representation of the species (see table 1). Control seeds could not be collected for all species as they could only be found in the forest when dropped by a gibbon or orang-utan being followed. Therefore non-*Ficus* control data was only collected for the genus *Artobotrys* and the species *Fibraurea tinctoria*.

For the genus *Artobotrys* neither control seeds nor seeds which had been defecated germinated. Control seeds for *Artobotrys* were only monitored for 5 weeks as they were collected relatively late during the period of study. For *Fibraurea tinctoria* a greater proportion of control seeds germinated than defecated seeds, within a 7 week period, however this difference was not significant, and the defecated seed sample size was small (N=10). There was insufficient data to compare the germination latency statistically. No non-*Ficus* seeds germinated from orang-utan faeces.

3.2.2 *Ficus* seeds:

3.2.2.1. Comparing Germination proportion for gibbon defecated seeds planted under 3 different conditions:

To compare the difference condition (*faeces*, *peat*, *petri*) made to germination proportion for *Ficus* seeds, it was decided to compare germination success within defecations only, due to the inability to recognize species, as this meant that it was much more likely that the same species or mixture of species was being compared. *Ficus* seeds from four gibbon defecations were planted in approximately equal numbers in the conditions *faeces* and *peat* (see table 4). Germination success was compared using a test for the difference in binomial proportions (Fisher's exact test).

Table 4. Comparing proportion germination in *peat* and *faeces*:

<i>Defecation</i>	<i>No. planted faeces</i>	<i>No. planted peat</i>	<i>Proportion germinated faeces (%)</i>	<i>Proportion germinated peat (%)</i>	P value (Fisher's exact test)
1	100	97	0	1.03	0.492
2	39	39	0	2.56	1.000
3	87	80	3.44	7.50	0.314
4	116	116	0	2.59	0.247

The proportion of seeds which germinated was very slightly higher for those in *peat* than those in *faeces* for each of the four defecation trials, however this difference was not significant for any of the defecations. To compare the difference between the conditions *faeces* and *petri*, seeds from four defecations were planted in approximately equal numbers where possible (see table 5), while to compare the effect of *peat* to the effect of

petri, *Ficus* seeds from two defecations were planted under the different conditions (see table 6).

Table 5. Comparing proportion germination in *faeces* and *petri*

<i>Defecation</i>	<i>No. planted faeces</i>	<i>No. planted Petri</i>	<i>Proportion germinated faeces (%)</i>	<i>Proportion germinated petri(%)</i>	<i>P value (Fisher's exact test)</i>
1	930*	100	1.82	1.00	1.000
2	160*	100	6.25	5.00	0.789
3	87	80	3.45	2.5	1.000
4	116	116	0	0	1.000

*estimated by counting no. of *Ficus* seeds in 4 g of the defecation

Table 6. Comparing proportion germination in *peat* and *Petri*:

<i>Defecation</i>	<i>No. planted peat</i>	<i>No. planted Petri</i>	<i>Proportion germinated peat (%)</i>	<i>Proportion germinated petri(%)</i>	<i>P value (Fisher's exact test)</i>
1	80	80	7.50	2.50	0.246
2	116	116	2.59	0	0.247

It can be seen from table 5 and table 6 that any difference condition made to germination proportion of *Ficus* seeds was not significant. To compare germination latency, a Kolmogorov-Smirnov test is usually used (e.g. McConkey 2000). However, <10 seedlings germinated in all but two samples, which were from different defecations and so could not be compared, therefore germination latency could not be compared overall.

3.2.2.2 Comparing germination proportion for orang-utan defecated seeds planted under different conditions:

Ficus seeds from 5 orang-utan defecations were likewise planted in the two conditions *faeces* and *peat* (see table 7).

Table 7- comparing germination proportion in *faeces* and *peat*:

<i>Defecation</i>	<i>No. planted faeces</i>	<i>No. planted peat</i>	<i>Proportion germinated faeces (%)</i>	<i>Proportion germinated peat (%)</i>	P value (Fisher's exact test)
1	127	128	4.72	3.90	0.769
2	76	56	1.31	0	1.000
3	91	91	2.20	2.20	1.000
4	159	159	2.51	0	0.123
5	87	87	1.15	0	1.000

Planting condition (*faeces* or *peat*) did not significantly affect the germination proportion. There was insufficient data for the condition *petri* for orang-utan defecated *Ficus* seeds as it was only decided that this condition be used half way through the experiment when it became clear that germination success was surprisingly low.

As with the gibbon *Ficus* data, to compare germination latency between the conditions a much greater number of seedlings would have to have germinated; <10 seedlings germinated in each condition for every defecation.

3.2.2.3. Comparing control seeds planted under the conditions *peat* and *petri*:

Control data for only one species of *Ficus* could be obtained: *F. Spathulifolia*. For each batch of fruit collected (N=4), seeds were planted under two conditions; *petri* and

peat. As above the germination proportion was compared within each sample, for the two conditions (see table 8).

Table 8: Comparing germination proportion for control seeds in *peat* and *petri*.

<i>Batch</i>	<i>No. planted peat</i>	<i>No. planted petri</i>	<i>Proportion germinated peat (%)</i>	<i>Proportion germinated petri (%)</i>	P value (Fisher's exact test)
1	50	50	0	2	1.000
2	100	100	1	0	1.000
3	100	100	0	0	1.000
4	100	100	0	14	0.000

For three of the samples the germination proportion is not significantly different for either condition; while for sample four using the Fisher's exact test there appears to be a significant difference for the two conditions. However if a Kruskal-Wallis ANOVA is used to analyze the data, overall the condition (*peat*, *petri*) does not significantly explain the variability in the data ($p=0.321$). It can be seen that, similar to the defecated seeds, the proportion of control seeds which germinated was extremely low.

3.2.2.4 Comparing orang-utan defecated seeds, gibbon defecated seeds and control seeds

To compare the germination proportions of seeds from different origins (orang-utan defecated seeds, gibbon defecated seeds or control seeds) seeds from several different defecations or batches planted under the same condition were compared using a Mann-Whitney U test (see table 9). This analysis is not as robust as those comparing within the sample, as it is possible that different species were being compared; however data could be used from those defecations where the seeds were only planted under one condition. At least 39 seeds were planted for each sample in the analysis; seeds from two orang-utan

defecations were excluded from germination trails as they comprised only 3 seeds in total. Overall, the difference in germination proportion between orang-utan and gibbon defecated seeds and compared to control seeds was not significant for any of the conditions (see table 9).

3.3 Growth analysis

The aim of the growth analysis was primarily to see whether growth of seedlings was affected by the condition they germinated under. Despite the fact that large numbers of *Ficus* seeds were planted, so few germinated per defecation that there is insufficient data to compare the effect of planting condition on growth statistically. In addition, seeds which germinated after 2nd of September were not planted as I left on this date (existing seedlings and germination plates were monitored until the 18th September) and sample sizes were further reduced by some seedlings being washed away in heavy thunderstorms. However, the high mortality of *Ficus* seeds compared to non-*Ficus* seeds is striking. Of the 12 defecated non-*Ficus* seeds (2 unknown, 1 *Willughbeia*, 3 *Syzygium*, 5 *Zyzyphus angustifolius*, 1 *Fibraurea tinctoria*) which germinated and were monitored for 21 days, none died. Likewise there was 100% survival for the three control seedlings (*Fibraurea tinctoria*) which were monitored. For those *Ficus* seeds defecated by either an orang-utan or gibbon and then subsequently planted in peat, 9 of 12 seedlings died within 21 days of germination (75.0%). For ape defecated seeds which germinated in faeces, 22 of 36 seedlings died (61.1%) and of the Gibbon defecated seeds germinated on Petri dishes, 11/21 seedlings died within the 3 week period (52.4%). Similarly, control seedlings had a high mortality; the one seed which germinated in *peat* and was monitored

died, while one seed which germinated in *petri* survived. Fig seeds from one *Petri* sample which was excluded from the main analysis since it was only monitored for 4 weeks rather than 7 had 100% mortality (N=5 seedlings). While the survival of seedlings between the different conditions may not be directly comparable, since the seedlings could be of different species, it is clear that seedlings from the genus *Ficus* have a high mortality within the first 3 weeks subsequent to germination.

3.4 Light intensity

A GLM ANOVA was carried out for the light intensity data from the seedling bench and the germination bench. Position on the bench was found to significantly explain the variability in the data for the germination trays ($P=0.000$); although the light intensity readings for each position were not hugely different (means for each position = 7.776, 8.662, 9.990 Ev), they were consistently different. For the seedling bench the position did not significantly explain the variability in the data ($p=0.835$).

4. Discussion

4.1 Gibbons and orang-utans as seed dispersers

The number of defecations analysed for each species, gibbon or orang-utan, was small due to the difficulty of collecting faeces. The 14 gibbon defecations analysed had significantly more species of seed on average per defecation than the 27 orang-utan defecations, and intact non-*Ficus* seeds occurred in a much higher proportion of gibbon defecations (100%) than orang-utan defecations (7.4%). In addition on average a larger number of intact non-*Ficus* seeds were found in gibbon defecations. This was surprising, as all the plant species which were found in the gibbon faeces are known to be eaten by orang-utans in the area (Cheyne unpublished). In addition, orang-utans eat a greater amount of food than gibbons, being substantially larger (Galdikas 1982), and therefore have significantly larger defecations so it would be expected that they would defecate more seeds. It is possible that the orang-utans destroyed the seeds of some species, spat them out or ate less fruit than the gibbons. However previous data collected at this location suggests that fruit comprises a similar proportion of the orang-utan and gibbon diet in the dry season; while it comprises 46% of the gibbon diet (Cheyne unpublished), fruit makes up 56% of the orang-utan diet (Harrison unpublished).

The data does seem to support the hypothesis that gibbons are relatively good seed dispersers (McConkey 2000; 2005) as while intact non- *Ficus* seeds were found in 100% of defecations, evidence of damaged seeds was only found in 28.6% of defecations. Orang-utans do not appear to treat seeds so well, as intact non-*Ficus* seeds were found in 7.4% of defecations while damaged seeds were found in 33% of defecations, giving a rough implication that more large seeds are damaged than consumed whole, as damaged

seeds were all non-*Ficus* species (see fig 2). This is quite different to the results from a previous study on seed dispersal by the same species of orang-utan, where it was concluded that they are good seed dispersers as 94% of defecations (N=101) analysed contained intact seeds, with few damaged seeds (Galdikas 1982). However, this data was collected in a study area consisting of several different forest types, mainly lowland dipterocarp forest, which is substantially different to peat swamp forest.

Overall, the defecation data has to be taken with some caution as firstly, only a small number of defecations were analysed and secondly, the animals were only studied during the dry season when the diet of both orang-utans and gibbons is composed of less fruit than in the wet season (Cheyne unpublished, Harrison unpublished) . It is therefore possible that any differences between orang-utans and gibbons as seed dispersers implied by this study could just be a result of the small sample sizes and time of year.

4.2 Germination of seeds

Four of the eight non-*Ficus* species found in gibbon defecations germinated within seven weeks; however sample sizes were extremely low for the remaining seeds and so it cannot be concluded that these species do not germinate within seven weeks of being defecated. The fact that some seeds germinated, however is positive proof that gibbons do act as dispersers for at least four plant species in the Sabangau region. Since only very few non- *Ficus* seeds were found in orang-utan faeces, none of which germinated, little conclusions can be drawn about the germination of non-*Ficus* defecated seeds by orang-utans. Ideally, seeds would have been monitored for longer than seven weeks, as some

large seeded tropical tree species can take much longer to germinate (e.g. McConkey 2000); this may explain why some species did not germinate.

It is difficult to assess the effect of gut passage on non-*Ficus* seeds, due to the lack of both control data and defecated non-*Ficus* seeds. However, for the genus *Artobotrys* and species *Fibraurea tinctoria* for which control data was collected, germination success was not significantly different between defecated and control seeds (although *Artobotrys* seeds did not germinate). This does not contradict other studies of seed dispersal, which have shown that while some species of seed are affected, either positively or negatively, by gut passage, others are not. A review of 95 studies into the effect of gut passage through a non-flying mammal found that 39% of plant species had enhanced germination success, 18% had inhibited germination success and for 42% of plant seed species gut passage made no statistical difference (Traveset 1998).

Some *Ficus* seeds from both gibbons and orang-utans did germinate within the 7 week period; however the proportion which germinated was always extremely low, independent of treatment. Control seeds showed comparably low germination rates, which proved statistically similar under analysis. Since *Ficus* seeds were defecated in such high numbers, and viability appeared not to be affected by gut passage, it can be assumed that both gibbons and orang-utans are important dispersers of the *Ficus* genus in this location. Primates have long been thought important dispersers for this genus; and in turn figs are considered a vital food resource for many primate species (Serio-Silva 2002; Serio-Silva and Rico-Gray 2003; Wrangham *et al.* 1993).

Other studies into the effect of gut passage on *Ficus* germination have variable results; it has been proposed that different *Ficus* species respond in different ways to gut passage

through a primate (Serio-Silva and Rico-Gray 2003). For example, one study into two *Ficus* species (*F. aurea* and *F. microcarpa*) concluded that germination was not affected significantly by gut passage through the Indian hill Mynah bird, *Gracula religiosa* (Kaufmann *et al.* 1991). However, another study found that some species of *Ficus* appeared to be unable to germinate without the effect of gut passage through a gibbon and of six species studied four had the germination proportion increased by gut passage (McConkey 2000). Similarly the germination success of *Ficus enormis* seeds is increased by passage through howler monkeys *Alouatta fusca* (De Figueiredo 1993).

As so few *Ficus* seeds germinated, germination latency could not be compared across treatment groups; but seeds did begin germinating from nine days after planting, indicating that the seven week monitoring period not being sufficiently long was unlikely to be a major explanatory factor for the low germination success. The *Ficus* genus is enormous, comprising 750 or more species (Compton *et al.* 1996) and is ubiquitous across the tropics. Germination rates across the genus do seem to vary; some of this variation no doubt due to differences in research method. However it does seem that the results shown here, with the defecated seed samples all having a germination success of <13% (total number of samples = 34), show an unusually low germination success. For example, in Barito Ulu, central Borneo, gibbon defecated *Ficus* seeds showed a germination success of 22-93% for the five out of six species which germinated (McConkey 2000). Similarly, howler monkey defecated *Ficus enormis* seeds had a high germination success of 87.4% (De Figueiredo 1993).

There are several reasons which may explain why the *Ficus* seeds showed such a low germination success. First, it is possible that their unusual, well documented, highly

specific pollinating system involving fig wasps (family Agaonidae) (e.g. Wiebes 1979, Janzen 1979) has been disrupted in this area, due perhaps to the logging which was only discontinued in 1997. Second, this pollinating system involves the loss of some seeds, possibly 50% or more in some species, to the fig wasp larvae which develop inside the seeds (Janzen 1979). As the seeds are so minute, a microscope is required to see which seeds have been damaged (De Figueiredo 1993; Serio-Silva and Rico-Gray 2003). Therefore this could account for the low germination success; to accurately assess the effect of gut passage on *Ficus* seeds, a microscope should be used to examine both defecated and control seeds and the damaged seeds discarded before germination trials (De Figueiredo 1993; Serio-Silva and Rico-Gray 2003). However, this would not be possible in the Natural Laboratory for Peat Swamp Forest, as there is limited equipment due to the damage which the humidity can cause to instruments such as microscopes. Many other studies involving the dispersal of *Ficus* seeds also did not use this methodology, presumably for the same reason (McConkey 2000, Knogge 2003, Laman 1995, Stevenson *et al.* 2002). Finally, since the seeds were germinated in a nursery and not under entirely natural conditions, it could be the case that conditions were not optimal for germination. However, several media were experimented with, none of which increased the germination success; in addition extensive research into the optimal conditions for *Ficus* seed germination has shown that the most critical factor is water availability (Laman 1995, Galil and Meiri 1981), of which there was plenty in the germination trays.

The planting condition did not significantly affect the germination proportion and there was not a significant difference between orang-utan and gibbon defecated seeds.

This may just be due to the seeds having extremely low germination and so subtle differences between samples were masked by variability in some unmeasured factor. However it seems clear that no striking difference to germination success was made by leaving the *Ficus* seeds in *faeces*. Another study which trialled different germination media, similar to those in this study, found that a significant effect was had on germination (Chapman 1989). However 26 plant species were studied; it may be that some species are affected to a greater degree by germination condition than others. For example, another study which trialled different germination media found that for four species germination was affected by substrate, while for one species it was not (Stevenson *et al.* 2002).

4.3 Seed size and Seedling mortality

Unfortunately, as germination success was so low for *Ficus* seeds, the effect of germination condition on later growth could not be established. However the planting of both non-*Ficus* and *Ficus* seeds did support the extensive literature regarding seed size and seedling mortality (review: Moles and Westoby 2004) as approximately half the *Ficus* seeds died within 21 days of planting, while there was 100% survival for non-*Ficus* species. Since all the non-*Ficus* seeds which germinated were >5mm diameter they can be classified as large seeds in this case, relative to the *Ficus* seeds. This highlights the different strategies employed by plant species to disperse their seeds, even when the same animal disperser is utilised. *Ficus* seeds which are produced in vast numbers had low survival subsequent to germination. This is presumably because each seed was of low quality compared to those species which produce one or two seeds per fruit and

consequently have higher seedling survival. Understanding the different trade-offs and strategies which plants employ to disperse their seeds is useful when considering the interaction between seed disperser and dispersed plant species.

4.4 Problems and method development

Several problems were encountered during the study. First, on two consecutive nights seeds were predated in the nursery, possibly by rats. Several of the larger seeds disappeared, and some were damaged (see table 1); this meant that already small sample sizes for the germination trials were further reduced. Rat poison was subsequently put out in the nursery which appeared to solve the problem. A second difficulty was that of seed identification; it was not even possible in some cases to distinguish seed fragments from intact seeds with complete confidence. Since this was the first study of primate seed dispersal in the area, there was not much existing knowledge about the identification of seeds from faeces. To try to solve this problem, unidentified seeds were planted, however not all of them germinated, and one species could not be identified once germinated. With a greater amount of time, many more controls could have been collected, which would have assisted in identification, and expertise could be built up. A third difficulty was that of counting the *Ficus* seeds, due to their extremely high abundance in some defecations which meant it was time consuming to accurately count them. It was therefore decided to experiment with counting the seeds in 4g of each defecation and to extrapolate the number counted to estimate the total number of *Ficus* seeds in each defecation. Since *Ficus* seeds appeared to be distributed fairly homogeneously in the samples this seemed a valid method and the results support this. In samples where seeds

were counted for the entire defecation each condition had very similar germination rates. Similarly, in those samples where the amount of *Ficus* seeds in the *faeces* condition was estimated (defecations 1 and 2 of table 5), statistically similar numbers germinated to the *petri* condition where the exact number of seeds planted was known. A fourth problem was that of collecting controls; since they could only be collected when being eaten by an orang-utan or gibbon, this meant that controls for only three species were collected. However, with a longer period of study, there would be adequate time for the collection for more control species. Finally, although the light intensity was assumed to be constant under the tarpaulin in the nursery for the germination plates, when this was measured in the 5th week of study, it was found that there was a difference between the sites measured. However, although the 3 positions were consistently different, the mean light intensity for each did not differ by very much and consequently is thought to have had very little effect on the germination of seeds, especially as the plates were moved regularly. For future studies in this nursery, the light intensity could be taken into account during the experimental design stage by techniques such as ‘blocking’. Overall, the methods used were effective, however a complete study into seed dispersal in this region by gibbons and orang-utans would have to be carried out over a period of at least a year, to encompass both the wet and dry seasons and to ensure sufficient sample sizes for germination and growth analyses.

4.5 Conclusions

Overall, the data seems to indicate that the gibbons in the Sabangau region disperse more seeds and damage a smaller proportion of ingested seeds than the orang-utans. Both

species disperse substantial numbers of seeds from the genus *Ficus*. Germination data for non-*Ficus* seeds is limited, due to the small initial sample sizes for each plant species, however four species germinated after passage through a gibbon gut. Control data for one species which did not germinate when defecated (genus *Artobotrys*) and one which germinated (*Fibraurea tinctoria*) did not show a significant effect of gut passage on germination success. *Ficus* seeds had a very low germination success, which did not appear to be influenced either by gut passage or planting condition. The seedling growth data supports much previous study on the relationship between seed size and seedling survival, as the small seeded *Ficus* seedlings had much higher mortality than larger seeded species. If the described methods were used over a sufficiently long period of study, at least a year, much could be learned about the relative interactions of gibbons and orang-utans with their environment in the Sabangau.

Acknowledgements

My thanks to Dr Susan Cheyne, my supervisor; also to Laura Graham who set up and runs the Sabangau Seedling nursery and Eben Eser for the identification of seeds.

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