A study of secondary seed predation and dispersal

in Bornean Peat Swamp Forest,

Central Kalimantan, Indonesia

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Abstract

This study, in the peat swamp forest of Central Kalimantan, Indonesia, considers secondary dispersal and predation by animals on the forest floor. Three tree species were selected, *Parartocarpus venenosus* (Moraceae), *Eugenia grandifolia* (Myrtaceae) and *Blumeodendron tokbrai* (Euphorbiaceae). Once their ripe fruit was displaced from the canopy by feeding orang-utans, predation rates by insects and terrestrial vertebrates were determined, which ranged from 17-75% after fifteen days. Time series analysis showed insect predation rates lagged vertebrate predation rates for *Eugenia* and *Blumeodendron*. For vertebrate predation, seed-fate was observed by attaching nylon threads to the seeds. The predation in-situ and removal rates were similar, unlike many tropical seed-fate studies where removal rates are much higher than predation in-situ. Removal distances were low (maximum 8.4m), with little evidence of caching. This differs from findings in other tropical forests suggesting the peat swamp forest is an unusual or unique ecosystem.

Key Words: Indonesia, peat swamp forest, insect seed predation, vertebrate seed predation, secondary dispersal, seed-fate.

Introduction

Overview of the role of seed predation and dispersal by animals in tropical forest

The hypothesis that seeds must be moved away from the parent tree in order to have better rates of survival was pioneered by Janzen (1970) (for survival of seeds) and Connell (1971) (for survival of seedlings). They suggested that based on density dependence, predator and pathogen pressure would decline further from the parent tree, thus increasing survival chances. Many studies have supported the Janzen-Connell hypothesis, though with differing reasons for its cause (Wilson and Traveset 2000). Further, Howe and Smallwood (1982) suggest that as well as this 'escape hypothesis', the seed's need to move away from the parent tree, there is also the 'colonisation hypothesis', the need to reach newly disturbed areas, and the 'directed dispersal hypothesis', to reach areas the plant is particularly adapted to.

Animals have been shown to be important dispersers, and may disperse the seeds internally or externally, actively or passively (Stiles 2000), through regurgitation, defecation, spitting the seeds out, or dropping them unharmed (Jordano 2000). Initially, avian and primate dispersal was considered most crucial and rodents were perceived primarily as seed predators. However, a seed-fate study by Forget (1990) using a thread tagging method, showed caviomorph rodents cached 70% of their seeds, whilst their retrieval was often significantly lower than 100%, thus leaving seeds dispersed and protected. Many more studies have found similar results (though not all, Wenny 2000), observing, after secondary seed dispersal, an increase in the removal distance and an improved microhabitat for the seeds, thus highlighting the important role of small mammals as seed dispersers throughout many of the tropical regions (for review see Jansen and Forget 2001). As work has moved away from just the neo-tropics, the caching behaviour of the small, terrestrial animals, acting as secondary dispersers, has been observed across three continents, and across differing evolutionary lines. This would suggest a convergent evolution, dependent upon a mutualism of the trees and their dispersers (Forget and Vander Wall 2001). If this is true, studies must continue across more tropical zones.

Small mammals act as predators as well as dispersers. 'Post-dispersal seed predation is frequently the major cause of plant mortality, and thus a key process to recruitment' (Nathan and Casagrandi 2004)

and the predation rates may be as high as 75-100% (Howe 1993). However, predation can be highly variable, with predation by birds and small mammals being affected by insect predation (Valberg 1992a, 1992b) and by fruiting phenology and fruit characteristics (Jordano 2000).

The potential importance of higher predation pressure close to the parent tree can be complicated by several factors. Insects are suggested to have a small range within which they predate and, as such, dispersal will allow the seeds to escape it, but terrestrial rodents have a much larger range and thus dispersal does not offer such an advantage (Howe 1993). It has, therefore, been argued that the insect predation near the parent tree should be more important than the wide ranging predation of rodents for the Janzen-Connell hypothesis to hold true (Nathan and Casagrandi 2004, Howe 1993).

Bringing together these concepts allows insight into forest community dynamics. Work would already hint that phenology of fruiting cycles can impact upon vertebrate life cycles (Jordano 2000), that the extent of dispersal by animals can affect the forest population dynamics (Wison and Traveset 2000) and diversity (Webb and Peart 2001), and has potentially already influenced the evolution of the trees (Forget and Vander Wall 2001).

Turning attention to Indonesia

Indonesia holds some of the world's most bio-diverse tropical ecosystems (Ashton 1993). The wet season falls from December to March with the dry season from May to September, in-between the seasons are seen as transitional and vary considerably. As such, the fruiting pattern of the non-masting trees (the area is predominantly dipterocarp forest – a family of masting species) is highly unpredictable, resulting in periods of scarcity and abundance (Leighton and Leighton 1984). The region has had only one seed-fate study of secondary seed dispersal by terrestrial mammals, carried out in Malaysia, considering the introduced oil palm fruit (Yasuda 2000). However, a theoretical study focussed in West Kalimantan suggests that animals serve a crucial role in maintaining the biodiversity of the forest, and the absence of the rodents could result in a 60% loss to total dispersion (Webb and Peart 2001).

One of Indonesia's diverse regions is the peat swamp forest, stretching over 3M ha of Central Kalimantan, Borneo, Indonesia. Little research has been carried out in peat swamp forest, possibly due to its difficult living terrain, and until recently most evidence for this area was anecdotal (Corlett 1998).

Within the forest there are many primary dispersers: gibbons and hornbills are considered some of the most important, others include tree shrews, pigs, deer, rodents, orang-utans and macaques (Corlett 1998). Orang-utans are known to act as significant seed dispersers, with a large range, and being non-specific in their food type preference (Corlett 1998). But, how crucial are the rodents and other small terrestrial mammals in swamp forest where the floor can be entirely submerged in water for several months of the year? Further, if the rodents of peat swamp forest do not cache, they instead may play a crucial part as predators, therefore placing more importance on the primary dispersers, specifically the primates and birds.

This study makes a preliminary investigation into the role of terrestrial predators of the seeds of the trees that have first attained primary dispersal by orang-utans. Orang-utans move from tree to tree throughout the day to feed on ripe fruit, leaves, bark and insects. As they feed, some of the fruit that has ripened on the tree falls to the ground intact, making it available to terrestrial predators/dispersers. Removal by terrestrial animals from under the parent shadow may increase survival, provided some is abandoned or cached.

Therefore, my study investigated this stage of the seed dispersal loop: Of the fruit initially predated/dispersed by orang-utans, which is most predated on the forest floor? What are the predation rates of the insects and vertebrates, and do the rates differ? Of those which are predated by vertebrates, are they predated in-situ or removed? If they are removed, what is their seed-fate, and is there evidence for caching? From the answers to these questions, what may be concluded about the ecology of the forest community and what are the implications for future studies?

Methods

Study site

The experiment was carried out in the Pt. Setia Alam Jaya timber concession, 20 km southwest of Palangkaraya. This expansive 9200km^2 of peat swamp forest is in the upper catchment of Sungai (River) Sebangau. The study site was a 3km by 3km research area, with access transects every 250m across the site, from north to south, and east to west.

Study species

Of the nine species known to be in fruit in the research area during July 2004, eight had their predation rates on the forest floor observed, see Appendix A. From this, *Parartocarpus venenosus*, *Eugenia grandifolia* and *Blumeodendron tokbrai* were selected as the study species. They were in high fruiting abundance, predated by orang-utans, and showed differing fruit characteristics (Table 1, see Fig 1 for photographs of the three species' seeds).

Table 1: Details of the fruiting tree species selected for the study.

Tree Species	*Parartocarpus venenosus*	*Eugenia grandifolia*	*Blumeodendron tokbrai*
Fruit characteristics	Large fruit with prickly ectocarp and thick layer of soft flesh. Medium sized seeds dispersed throughout flesh, ranging from 2-18 per fruit.	Small fruit with soft flesh, with 4 small seeds at centre.	Tough thick ectocarp, with thin layer of flesh surrounding 3 large seeds with thick testa.
Seed characteristics on the forest floor	Flesh fell away as fruit hit the floor, leaving exposed individual seeds.	Seeds remained enclosed in flesh.	Seeds remained enclosed in ectocarp
Approximate no. fruit dislodged after an orang-utan feeding event	100	50	50
No. of tree individuals used in the study	4	5 (though with total of 6 seed data sets, as one tree was time replicated)	5
Number of sets per tree	4	4	4
Exact number of seeds per set	25	12	12

N.B. Although some of the seeds remains inside the fruit during their potential dispersal, and as such should be technically referred to as diaspores, for the purposes of this study they are referred to as seeds.
N.B. See Appendix B for data on each tree individual.

Fig 1: Photographs of each of the seeds used in the study. a) and b) show seeds of *Parartocarpus,* a) in the state it was collected from the forest floor, with some of the fruit's flesh still attached, and b) showing the signs of vertebrate predation. c) and d) show *Eugenia* seeds laid out in sets. c) shows a threaded set, d) an unthreaded set. e) and f) show seeds of *Blumeodendron*, e) in the form it was found on the floor, f) after it has experienced vertebrate predation (two of the three seeds remaining).

Seed predation and dispersal

Of the seeds that were collected from the floor after an orang-utan feeding event, half were used to make two threaded sets and the other half were used to make two non-threaded sets. This allowed predation rates between the threaded and non-threaded sets to be compared. If there was a significant difference between these rates, only the non-threaded sets, as the 'natural' sets, could be used to give the true predation rate, the threaded set data could be used only in establishing seed-fate. To make the threaded sets, 1m long pieces of white thread were sewn through the testa of the seed or through the tough ectocarp; the other end of the thread had a material identification tag attached. The seeds were then returned and placed around the parent tree (Fig 2). The position of each seed allowed it to be identified, but to the seed predator the layout was similar to that found naturally. Above each set, the vegetation density percentage cover was measured using a segmented eye-piece, at heights of 0-5m, 5-10m, 10-15m, and 15+ m.
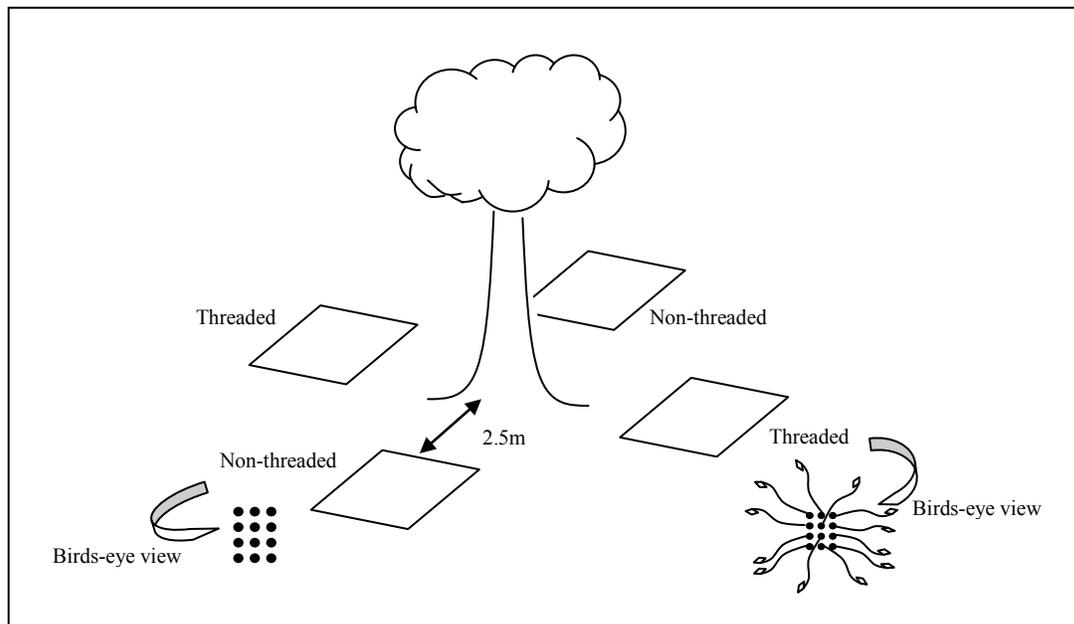

Fig 2: Diagram of the layout of threaded and non-threaded sets around the parent tree. Diagram showing 12 seeds per set is in accordance with the abundance of *Eugenia* and *Blumeodendron*. For *Paratocarpus* seed sets would each contain 25 seeds.

The sets were checked every three days for fifteen days and recordings made (Table 2). After a threaded seed had been removed, a search was conducted for the thread, with 10m radius from the set. Thick undergrowth prevented searching at any greater radius to any degree of accuracy (most studies search 20-30m from parent tree, however, few seeds are found beyond 10m (Forget 1990)). At the site of recovery (the deposit site) it was recorded whether the seed was cached or predated. The vegetation

densities of the forest above the deposit site were also recorded, thus the vegetation densities of where the vertebrates removed the seed from (the source site) and taken to can be analysed, showing if there is preference to predate under high vegetation density.

Table 2: Description of the type of recordings made when inspecting the seed sets, plus associated assumptions.

Set type	Observation	Recorded as	Assumptions	Validity of assumptions
Non-threaded	Seed no longer in set	Vertebrate predated	• There are no insects that *remove* seeds in this forest • Once removed, the vertebrate predates the seeds. • Before removal there were no insects in fruit	• None have been recorded to date. • This was true for nearly all threaded sets, where seed fate could be observed. • Work in this study showed after insect predation, vertebrate predation appeared much lower.
	Infested with insects	Insect predated	Infestation by insect prevented seed from germinating	Opening of infested seeds revealed extensive decay
Threaded	Seed no longer in set, thread remaining	Vertebrate predated in-situ	Before removal there were no insects in fruit	Work in this study showed after insect predation, vertebrate predation appeared much lower.
	Seed and thread no longer in set	Vertebrate removal	Before removal there were no insects in fruit	Work in this study showed after insect predation, vertebrate predation appeared much lower.
	Infested with insects	Insect predated	Infestation by insect prevented seed from germinating	Opening of infested seeds revealed extensive decay

Statistics

To analyse the variation between rates of predation for threaded and non-threaded sets for each tree species, paired-wise t-tests were used. Insect predation rates and vertebrate predation rates were analysed separately. To show whether any interaction occurred between insect and vertebrate predation, chi-squared tests were used. The predation rates of the insects and vertebrates were examined using time series analysis. For all the models that were used to fit the curves of summed predation rates, the residual levels and normal distributions were legitimate.

Comparison of predation in-situ versus removal rates for each tree species was done with pair-wise t-test. Further, using pair-wise t-test, comparison of the vegetation density at the source site and the deposit site was carried out.

Results

For original data, see Appendix C for recordings from seed sets and Appendix D for recordings from seed searches.

Differences between threaded and non-threaded sets

For all species of tree studied, vertebrates displayed a significant, or a marginally significant preference, either for or against the threaded sets (Table 3). As such, only the non-threaded data can be used in predation rate analysis.

Table 3: Summary of analysis for threaded versus non-threaded sets. Showing p-values for paired t-test and preference. For non-summed data see Appendix E.

Tree	Predator	Threaded sets		Non-threaded sets			
		Number of seeds predated (summed total)	%	Number of seeds predated (summed total)	%	p-value	Preference
Parartocarpus	Insect	59	37	19	12	0.300	None
	Vertebrate	24	15	7	4	0.042	Threaded sets
Eugenia	Insect	64	45	52	37	0.152	None
	Vertebrate	13	9	51	36	0.005	Non-threaded sets
Blumeodendron	Insect	19	16	11	9	0.338	None
	Vertebrate	16	13	43	36	0.051	Non-threaded sets

Predation

Insect and vertebrate predation was observed on all tree species, though predation after fifteen days varied considerably (Table 4).

Table 4: Predation rates observed on non-threaded sets.

	Just insect predated		Just vertebrate predated		Predated by both insects and vertebrates		No predation	
Tree	No.	%	No.	%	No.	%	No.	%
Parartocarpus	19	12	7	5	0	0	134	84
Eugenia	52	37	52	37	2	1	36	25
Blumeodendron	10	8	42	35	1	1	67	56

Given the rates of predation observed by both insects and vertebrates, the frequency of observed predation by both of these predators on any one given seed was at least marginally significantly lower then expected for *Eugenia* and *Blumeodendron*, revealed with chi-squared (Table 5).

Further, for *Blumeodendron*, comparing the ratio of actual predation rates between insects and vertebrates to the ratio predicted from the expected predation rates in the chi-squared analysis, the actual vertebrate predation was significantly higher than the actual insect predation (p=<0.005). For *Eugenia* the predation rates of insects and vertebrates were equally weighted, and so within the expected ratio.

Table 5: Chi-squared analysis results of relationship between insect and vertebrate predation.

Parartocarpus		Vertebrates	
		Not predated	Predated
Insects	Not predated	134	5
	Predated	19	0

p-value = 0.995

Eugenia		Vertebrates	
		Not predated	Predated
Insects	Not predated	36	52
	Predated	52	2

p-value = <0.001

Blumeodendron		Vertebrates	
		Not predated	Predated
Insects	Not predated	67	42
	Predated	10	1

p-value = 0.052

Time series analysis

The timing of insect predation and vertebrate predation during the 15 days of study was different (Fig 3.a and Fig 4.a). Time series analysis was performed on the data for only *Eugenia* and *Blumeodendron*, as *Parartocarpus* did not show difference in chi-squared analysis. High rates on vertebrate predation occurred before high rates of insect predation.

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For *Eugenia,* using models of best fit, vertebrate predation rate followed an S-shape curve (Fig 3.b), with initial low rates of predation, then an increase such that the predation level was higher than the insect predation, but then predation rates slowed again – such that insect predation was greater on the last day. Insect predation followed an increasing quadratic curve (Fig 3.c), with initial slow rates of predation increasing throughout the fifteen days. For *Blumeodendron*, the vertebrate predation rates followed a decreasing quadratic curve (Fig 4.b), with initially high rates of predation, with lower predation at the end of the two weeks. The insect predation rate followed an increasing quadratic curve (Fig 4.c) starting slowly, with predation rates increasing at the end of the two weeks.

Determining seed-fate

Eaten in-situ versus removed

Unlike many other studies, high levels of in-situ predation by vertebrates were observed, such that there was no significant difference between the levels of predation in-situ versus the removal rate (Table 6). There is, perhaps, a slight indication that levels of in-situ predation would be significantly higher than removal rates, but more tree individuals would need to be included; the sample size analysed is very small.
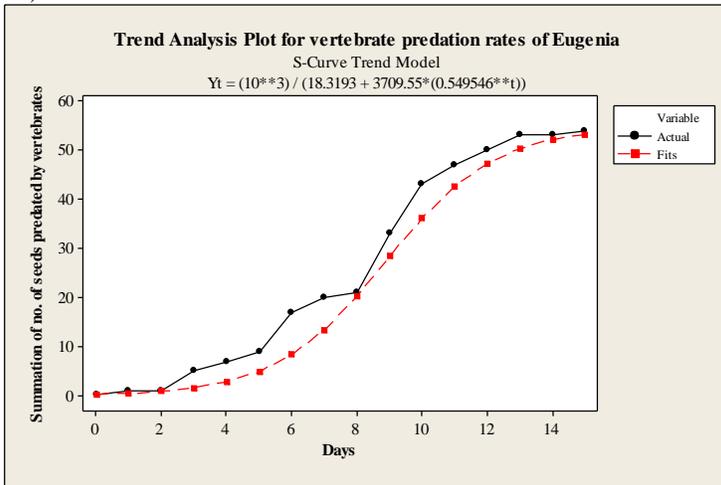
Table 6: Showing summed levels of predation in-situ of vertebrates, versus the removal rates. The p-values of the paired t-test for the predation in-situ versus removal rates are also given.

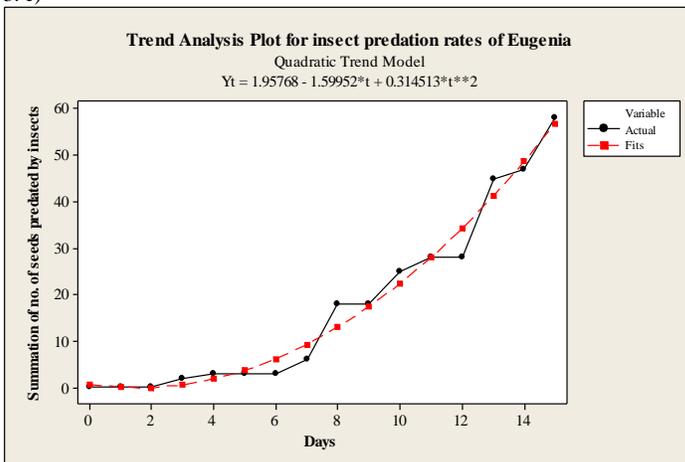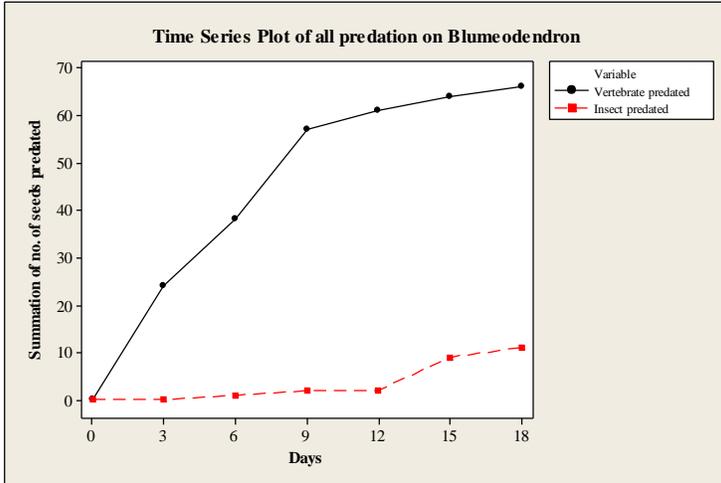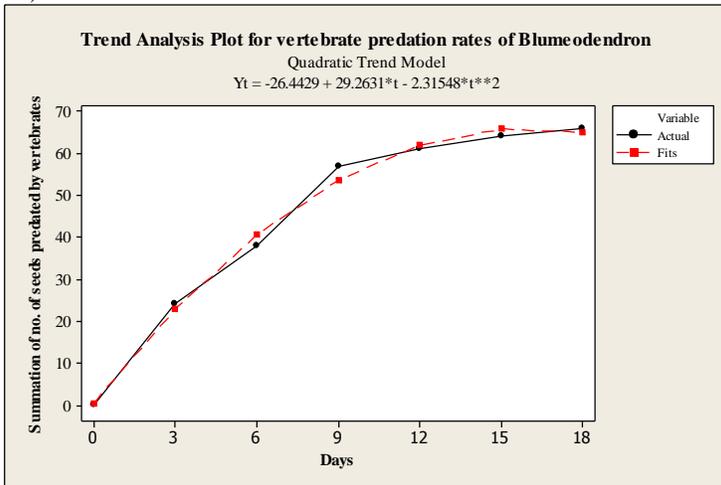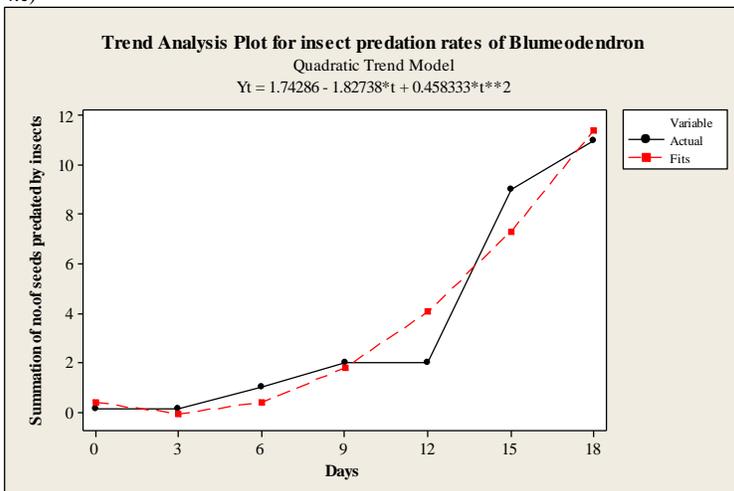| Tree	Number of seeds predated in-situ	Number of seeds removed	p-value
Parartocarpus	13	11	0.351
Eugenia	7	6	0.791
Blumeodendron	10	6	0.726

3. a)
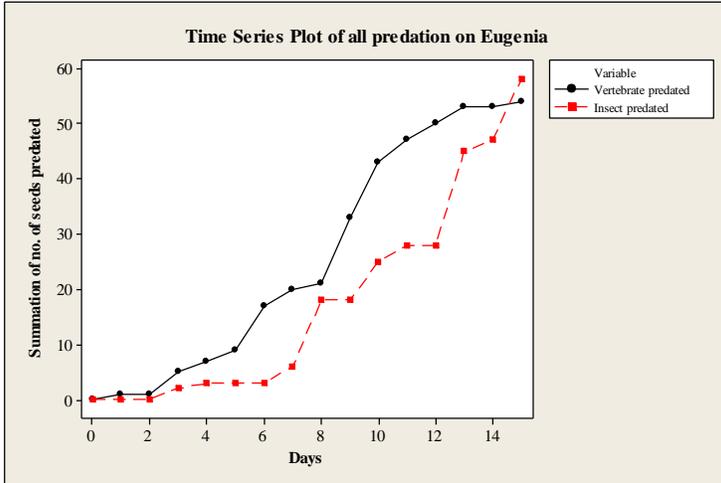
3.b)

3. c)

Fig 3:a) Showing the time series curves of summed predation rate for both insects and vertebrate, b) and c) show the nature of the two different curves, showing their shapes to be distinct.

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4.a)

Time Series Plot of all predation on Blumeodendron

4.b)

Trend Analysis Plot for vertebrate predation rates of Blumeodendron
Quadratic Trend Model
$Yt = -26.4429 + 29.2631*t - 2.31548*t**2$

4.c)

Trend Analysis Plot for insect predation rates of Blumeodendron
Quadratic Trend Model
$Yt = 1.74286 - 1.82738*t + 0.458333*t**2$

Fig 4: a) Showing the time series curves of summed predation rate for both insects and vertebrate.
b) and c) show the nature of the two different curves, showing their shapes to be distinct.

Recovery of removed seeds

Conducting seed searches for the removed threaded seeds gave a recovery rate of over 70%. Of the removals, 38% were removed less than 1m from the set. Distances of recovery from the source set ranged up to 8.4m. Threads were discovered sticking out from holes, the seed eaten down the hole. A larder-hoard cache (with multiple seeds) was discovered in *Eugenia* and a scatter-hoard cache (with single seed) was discovered in *Parartocarpus*. In two instances, threads were discovered in the branches of saplings, once for *Eugenia* and once for *Blumeodendron* seeds.

The vegetation density at the different forest heights (0-5m, 5-10m, 10-15m, 15+m) was recorded at the source sites and deposit sites, when the seed was removed and consumed still on the forest floor. Vertebrate predators showed a preference for removing the seeds to areas of higher vegetation density (for data from the 0-5m height range, see Appendix F), p-value = 0.091. It is believed this value would have been significant were it not for the small sample size, Fig 5. The small sample size was due to many of the removals being less than 1m removed, up trees and that there was an aversion against threaded sets for two of the three species.
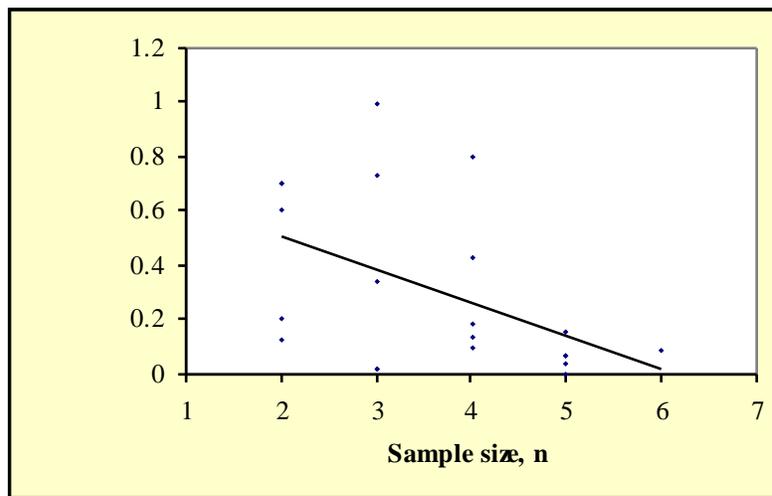

Fig 5: Relationship between the sample size of seeds removed and associated p-value for pair-wise t-test of vegetation density at the source site and deposit site. The vegetation density at the source site and deposit site was recorded to show if there was a preference for removing to a relatively higher vegetation density. Using pair-wise t-test on the entire original data set, the p-value = 0.091, however the sample size was very small. The above boot strapping technique illustrates that as data was randomly selected from the original data set (five randomly created 'data sets' for each sample size), the p-value approaches significance with increasing sample size.

Discussion

Differences between threaded and non-threaded sets

For all three tree species used in this study, the vertebrates showed a preference either for or against threaded sets. With *Parartocarpus* the vertebrates preferred the threaded, for both *Eugenia* and *Blumeodendron* vertebrates preferred the unthreaded sets. If the vertebrates were locating the seeds by smell, the piercing may have increased the ease with which it was found, or, possibly, they would go to investigate the unusual threads. Avoidance of threaded sets is more understandable; mammals may be wary of objects not encountered before. Further, as the understorey of the forest is dense and rooty, trying to remove a seed with a long thread attached may have proved too difficult. However, there is less evidence for the latter; many of the fruits were eaten in situ, so removal would not be a consideration. Further, if the difficult terrain were the cause, threading would have been found snagged on obstacles with fruit removed just a short way – very few instances suggest this.

Entire sets were rarely eaten, suggesting food was not scarce at the time. If vertebrate predators had enough food, it allowed them to be selective for what they knew best. The fact that studies of other species elsewhere did not observe a preference for non-threaded seeds is perhaps unusual, and, possibly, fruit then was not abundant. One study did observe higher insect predation in threaded seeds (Forget and Milleron 1991), probably due to the pierced testa allowing easier access.

Due to aversion against threaded seeds, analysing the results of seed-fate and removal distances proved difficult with low sample size.

Predation rates and time series analysis

Many studies have shown that post-dispersal predation is the fate that befalls many seeds in forest communities, and this study is no different. With very little evidence of caching in the threaded sets, it can be assumed the majority of seeds missing from the non-threaded sets were predated. Insect predation rates ranged from 8-38%, vertebrate predation rates from 5-38%, the remainder still untouched after 15 days.

Vertebrate predation occurred at a higher rate than insect predation in two of the three species studied, *Eugenia* and *Blumeodendron*. It is possible that the sensory signals used to locate the fruit are

different for the different animals. As the fruit is adapted to attract primates, elaiosomes (oil bodies) may be used, to which mammals are sensitive, allowing faster location (Stiles 2000). Further, studies with agoutis have shown they can locate food dropping to the ground by sound, moving to that area of the forest (Stiles 2000). This may be of particular importance to this study as orang-utans, when feeding, often 'pop' the seeds in order to reach the nutrient-rich endocarp. This sound carries easily through the forest and mammals may follow the sound to where the orang-utans are feeding. Insects may be more adapted to locating the fruit at a more ripe stage, as this is when the fruit will be softer and require less energy expenditure to get through the ectoderm.

Insects may have located the fruit earlier than was observed and laid eggs in it, as observed in other studies of insects as fruit predators (Valberg 1992a, 1992b). The fruit can only be seen as predated once the eggs catch. Thus the predators may detect the fruit in unison, but the insects take longer to become apparent. For *Eugenia* the insects' rates of predation appear to come in bursts (Fig 2.a); periods of low predation followed by periods of high predation. This could signify the breeding periods of the insects; for example, the fruit fly has a breeding cycle of 10 days in temperate regions, possibly speeded to 8 days with elevated temperatures. However, it may also coincide with fluctuations in the weather. Weather, a variable not considered here, could impact heavily on insect predation rates.

The second possibility, rather than factors specific to each predator guild, is a direct interaction between insects and vertebrates. On a basic level, insects predate fruit less when it has been cached (Forget 1990, Forget and Milleron 1991). Further, due to range differences between insects and vertebrates, dispersal results only in escape from high insect predation (Howe 1993, Wenny 2000). As such, redistribution of seeds by vertebrates may reduce the amount of predation insects may cause.

However, other studies have also shown that if insects arrive first, they can influence the predation rates of the vertebrates. Some work shows avian frugivores will avoid infested fruits (Traveset 1993), whilst others show that it depends on the fruit that is infested. Chemical changes to the fruit such as fermentation were suggested as a cause (Valberg 1992a, 1992b).

This study suggests the insects find the fruit more slowly, or at least there is a lack of their apparent presence compared to the vertebrates, but once insect predation increases, vertebrate predation reduces. This is a very interesting aspect of the study, as none of the insects act as dispersers. Thus any

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dispersal by terrestrial animals must take place shortly after the fruit has been displaced from the tree (similar findings by Howe 1993). After this, it no longer is appealing to the terrestrial vertebrates, either through changes in the fruit, of through the arrival of insects, and then suffers the non-beneficial insect predation.

Determining seeds fate: Eaten in-situ versus removed and recovery of the removed seeds

It was hoped this study would show how many seeds were removed from under the parent's tree shadows, and once removed, whether these seeds were eaten, cached or abandoned. However, due to the preference by the vertebrates for non-threaded sets, the number of threaded seeds actually removed was quite low, just six seeds for both *Eugenia* and *Blumeodendron*. Therefore, only provisional conclusions may be drawn.

In this study, there was no significant difference between the predation rates of vertebrates eating the seeds in-situ and those removing them (Table 5). Other studies show very high removal rates of seeds from under the parent tree, often 70-100% disappear in just a few days (Forget and Milleron 1991, Yasuda 2000). Very few studies record levels of predation in-situ, and those which do usually record much lower predation in-situ than the removal rates (Wenny 2000). The reasons for the different patterns in this study may be due to the unusual living environment created by the swamp forest.

Due to the nutrient poor soil and the water-logging, the trees cannot grow as tall in this forest compared to dry forest. For example, this study site was in low-pole forest, yet a very similar species composition of trees, though of higher diversity, can be found in the tall-pole forest. In the tall-pole the water level is lower and there are more nutrients available. These trees may be 10-20m taller than their low-pole counterparts (MacKinnon et al 1997). Further, concession logging occurred at this site for 35 years, stopping less than 15 years ago. As a result, the largest and tallest trees have been removed, leaving gaps allowing the understorey to flourish. Due to the flooding, many trees are water adapted, with tall buttress roots, and extensive root systems, including stick roots, knee roots and stilt roots, leaf litter falling onto the elevated roots creating extensive tunnels. All these factors mean that terrestrial animals are often well protected and hidden from view, or, if not, cover is rarely more than one metre away.

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Thus a possible hypothesis for the high levels of predation in-situ is that vertebrates do not feel as exposed on this forest floor. At the deposit site, the vegetation density was higher than at the respective source site. Further, some threads were recovered from up trees, suggesting vertebrates that are both terrestrial and arboreal may, after encountering the seeds on the floor, move with it up the tree to avoid predation. Tags were also discovered sticking from holes. All these instances indicate that rather than the high levels of predation in-situ resulting from no cause to hide, there was still a real need to protect themselves from predators such as the clouded leopard (*Neofelis nebulosa)*, but that usually the protection close by was sufficient. This preference towards high vegetation cover has been observed in other studies (Forget 1990, Forget and Milleron 1991). To appreciate if the cause of high predation in-situ was due to the swamp forest environment, doing cross-site analysis between this site and areas in the tall-pole (where understorey variation is much lower) could provide revealing insights.

A second potential reason for the low removal rates is that, in other studies, high removal rates were associated with a high caching rate, and caching would occur at a particular microhabitat (Jordano 2000). If the terrestrial vertebrates in this region do not often cache, then the need to remove the seed and find a suitable habitat is reduced. The reduced caching may again be due to the environment of the peat swamp. If fruit is cached to be recovered during times of food scarcity as suggested by Forget (1991) then if the ground becomes flooded before or during this time the loss of caches may be more costly than the gain if they do survive. Further, due to the unpredictable weather and fruiting seasons, and the forests masting patterns, it is likely, while food overall is abundant, most of the terrestrial feeders are still generalists (though with some specific preferences) and therefore able to make use of whatever is available at the time.

The lack of caching was observed over a short time period. Caching is often seasonally effected, and it is possible caches are formed at other times of the year. As such, it cannot be assumed the animals in this area do not cache.

Within this area of the study, there is much room for expansion, most importantly, to discover what is doing the removing and whether removal causes seed death. Given the time available, only the distinction between vertebrate and insect predators was possible, but within this forest these vertebrates could include birds, rodents, tree shrews, pigs and deer. Further, in many fruits predated by birds or

primates, the seeds can tolerate being passed through the digestive tract, and, in fact, some require this to undergo germination (Jordano 2000). If any of the seeds were predated whole, a possibility for *Eugenia*, then internal passive seed dispersal may be occurring; this was beyond the scope of this study.

Implications to ecology and future work

Seed dispersal and predation are invariably crucial aspects to tropical forest regeneration, maintenance of biodiversity, and control of population dynamics. We now need to learn to piece together our fragmented understanding of studies of seed dispersal and predation, and those considering vegetation dynamics and plant distribution, in order to conserve these unique ecosystems. We should be able to compare what the dispersers appear to achieve and what actually comes to fruition.

To fully understand the dispersal loop, we cannot rely on just short-timescale studies. Evidence would suggest abiotic variation across years can have a larger and more significant impact than the impact of the seed dispersers in one year (Levey and Benkman 1999). Especially as Borneo has an unpredictable weather pattern, with wet and dry seasons shifting in time through the year. This leads to a highly variable fruiting pattern, and periods where there is fruit scarcity or fruit abundance (Leighton and Leighton 1984). It has been suggested that when particular fruits are not constantly available, this would lead to more generalist feeding (Smythe 1986), introducing more variability into the chance of secondary seed dispersal for the tree, and a potentially less close evolutionary mutualism between disperser and tree (Forget and Vander Wall 2001). The full implications of this can only be established through long-term studies such as Herrera's 12 year project (Herrera 1998).

This short study carried out in peat swamp forest of Central Kalimantan, Indonesia, illustrates that there is much to be learned, which cannot be extrapolated from other studies. A vast number of fruiting tree species and primary seed dispersers (gibbons, macaques, squirrels, birds etc) were not studied here. Further, only external active dispersal by secondary dispersers was considered. Yet, even within the three tree species considered, the results attained showed distinct findings. Preference between threaded and non-threaded sets differed across tree species, as well as the predation rates of both insects and vertebrates.

This study would suggest that once fruit reaches the forest floor, movement occurs only over a short distance and removal is rare. Caching appears infrequent and though convergent evolution of scatter-

hoarding seed dispersers may be occurring around the globe, there is little evidence for it here. Instead, most seeds suffer predation or must germinate where they fell. In this forest, insects, which show a delay in finding the seeds compared to the vertebrate counterparts, have enough time to locate the seeds and predate them as they are not removed at an earlier stage.

Studies have revealed that if seeds are dispersed along the forest floor by animals, the seedling survival can greatly increase. If, in this forest, secondary dispersal is not efficient or reliable there must be other means of escaping from under the tree shadow as the forest does remain healthy and diverse. For the trees with fruit adapted to vertebrate dispersal (as all in this study were), this would shift the importance back to the primary disperser, in this case, the orang-utans.

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