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The influence of gibbon primary seed shadows on post-dispersal seed fate in a lowland dipterocarp forest in Central Borneo

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Abstract: The natural seed shadow created by gibbons (*Hylobates mulleri* × *agilis*) in Central Kalimantan, Indonesia, was monitored over 11 mo to discern the role of gibbons and post-dispersal events in the spatial pattern of seed germination. Variability in the content and distribution of 183 scats was used to determine which, if any, scat characteristics influenced seed fate. Nine scat characters were evaluated: (1) seed number; (2) number of seed species per scat; (3) scat weight; (4) seed load; (5) rainfall; (6) scat density; (7) distance to nearest fruiting tree; (8) ripe fig abundance; (9) non-fig fruit abundance. More than 99% of monitored seeds were killed, removed, or had germinated during the monitoring period. Vertebrates killed or removed most seeds (86%) and the probability of them moving seeds was highly dependent on non-fig fruit abundance at the time of deposition; factors (2), (6) and (7) also influenced seed removal/predation by vertebrates, depending on whether seeds were deposited in peak or non-peak times of consumption. Insect predation (2% of seeds) occurred mainly in scats that were deposited in months of high ripe fig abundance, while the actual chance of a seed germinating (11% of seeds) was influenced by non-fig fruit abundance at time of deposition and number of species in the original scat. The gibbon-generated seed shadow was profoundly altered by post-dispersal events and variation in the characteristics of the shadow had little lasting impact on the probability of seeds germinating.

Key Words: Borneo, gibbons, *Hylobates mulleri* × *agilis*, Indonesia, Kalimantan, post-dispersal seed predation, seed fate

INTRODUCTION

Frugivores consume fruit and may either spit out the seeds or deposit them in scats. Only a few of these seeds survive the sequential post-dispersal stages (seed deposition, secondary dispersal and/or seed predation, seedling emergence) to become established seedlings (Blate *et al*. 1998, Byrne & Levey 1993, Hulme 1998, Sánchez-Cordero & Martínez-Gallardo 1998). It is generally assumed that frugivores can have a direct influence on seed fate, because it is the spatial traits of the initial seed shadow they generate that determine the vulnerability of seeds to post-dispersal events (Andresen 2002, Jordano & Herrera 1995, Julliot 1997, Nathan & Muller-Landau 2000, Wenny 2000). However, the intensity and variability in the selective pressures that operate at the various post-dispersal stages (Jordano & Herrera 1995, Rey & Alcántara 2000) have the potential to completely override primary seed shadows. Hence, it is possible that frugivores have very little influence on the final spatial aspects of seedling establishment.

Primary seed shadows are frequently complex, with scats from an individual animal containing variable numbers of seeds and species and being found in a diversity of locations (Fragoso & Huffman 2000, Julliot 1996, McConkey 2000, Wehncke *et al*. 2003). The few studies that have linked frugivore seed shadows directly with post-dispersal seed fate usually mimic limited aspects of these seed shadows experimentally (Andresen 2002, Calviño-Cancela 2002, Jordano & Herrera 1995, Rey & Alcántara 2000). However, it is difficult to devise experiments that consider all possible factors, or interaction of factors, that may determine a seed's fate. Monitoring of natural seed fall will provide a more complete initial assessment of the degree to which a frugivore influences seed fate and possibly suggest further avenues for detailed experimental studies.

Gibbons (Hylobatidae) are amongst the most important seed dispersers inhabiting forests in South-East Asia. Between 57 and 72% of their diet is fruit (Chivers

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1984 and references therein, McConkey *et al.* 2003) and virtually all seeds are dispersed in a viable condition in their scats (McConkey 2000). Gibbon defecations are variable in terms of content and deposit site (McConkey 2000), allowing a test of which aspects, if any, affect levels of post-dispersal activity and seed germination. I recorded the fate of seeds in a natural gibbon-generated seed shadow to discern the role of gibbons and initial post-dispersal processes through to seed germination. My aim was to determine whether the composition and spatial pattern of the seed shadow generated by gibbons directly influenced seed fate.

STUDY AREA

Field data were collected at the Barito Ulu Research Area (BURA) in Central Kalimantan, Indonesia from October 1996 to September 1997. BURA occurs virtually at the geographic centre of the island of Borneo (0°12′N, 114°6′E), in the watershed of the upper Barito River. The area has a rugged, hilly to mountainous terrain, with altitude ranging from 100–350 m asl. The main forest type is lowland dipterocarp forest, interspersed with heath forest (Brearley *et al.* 2004). The wet season at BURA usually occurs between October and January (fruiting also peaks during this period) and the dry season from July to August (J. Proctor *et al.* unpubl. data). These seasons were pronounced during the study period, but rainfall was markedly less overall (2585 mm in 1997) than in other years (mean annual rainfall was 3738 mm between 1990–96), due to a severe El Niño-induced drought in the last 3 mo of the study period. Mass-flowering of dipterocarps occurred near the end of the study period, but fruit did not appear until after the study ended. Bearded pigs (*Sus barbatus* Müller) also migrated through the study area in April–June 1997, which caused a drastic rise in numbers. During the migration pigs were at a density of 17 individuals km^{-2}, but before the migration the only evidence that pigs were resident in the area was occasional pig tracks (McConkey & Chivers 2004). It is likely that increased levels of post-dispersal seed predation by pigs occurred during the migration.

METHODS

Gibbon (*Hylobates mulleri* × *agilis*; Marshall & Sugardjito 1986) scats were collected opportunistically from October 1996 to May 1997, while following two gibbon groups for a total of 10 d mo^{-1} (see McConkey 2000, McConkey *et al.* 2002a for methods). All scats and gibbon feeding trees were mapped. Collected scats were described and then returned to the specific deposit site, which was marked by flagging tape tied 1.5–2 m above the forest floor (flagging tape was present for 1–2 d prior to scats being returned to the site). The distance to the crown of the nearest fruiting tree of any species (determined from feeding studies being conducted at the same time and searches in the immediate area) was recorded. The scat maps were used to determine the density of scats in 0.25 ha. While this is not an absolute scat density, the sample does identify regions that receive large numbers of gibbon scats each month, due to the use of routine travel pathways by the gibbons, and therefore may attract foraging seed predators.

Seed species present in the scats were identified from collections made of the gibbon feeding trees. When I was certain that complete scats were collected, the seeds and species were also counted, and the total scat weighed. Scats were never directly handled, but manipulated within a clear plastic bag. This was to ensure scats were not returned to the sites with the presence of human scent, which could increase rates of predation in the short term. Small seeds (< 5 mm diameter) were not counted or monitored since this would have involved direct handling of the scats. The spatial pattern and content of scats are described in McConkey (2000).

A total of 1470 seeds from 183 scats (at least 54 species) was returned to the forest and seed fate noted after 1 wk and then at monthly intervals for the remainder of the study period (4–11 mo depending on when scat was deposited). In each visit I recorded the number of seeds that had been destroyed by vertebrates (indicated by remaining seed fragments), destroyed by insects (indicated by bore holes in the seed testa), removed, or germinated (germinated seeds were also monitored until the end of the study period, but are not noted further here). Despite the variable monitoring time 99.6% of seeds had germinated, or been removed or killed by the end of the study; hence, seed fate to germination could be ascertained. Dung beetles also removed seeds in this study. No direct study of this was made as rates of removal appeared to be low during the time of study (McConkey 1999), but when seedlings of species that had been removed in the first week of monitoring appeared at the defecation sites I attributed these to burial by dung beetles (these seeds are included in the germinating seeds category).

One thousand trees were selected for monitoring fruit availability using the point-centre-quarter method (PCQ) (Mueller-Dombois & Ellenberg 1974). The four closest trees (one per quadrant) with dbh (diameter at breast height) greater than 10 cm were selected from a point every 20 m, along transects (totalling 5 km) running through the study area. All *Ficus* plants (118 in total) that could be observed from these trails were also marked and monitored for fruit. In 1 wk each month the trees, *Ficus* and all visible lianas present in the trees were monitored for fruit, by the same two observers. Density of trees with fruit, each month, was calculated (see McConkey *et al.* 2003 for a more complete description).

Data analyses

The influence of scat characteristics on three aspects of seed fate (the dependent variables) were assessed using logistic regression: (1) predation or removal by vertebrates in the first week. Removal and predation are grouped in the analysis, although removal may signify secondary seed dispersal (Yasuda *et al.* 2000). In West Kalimantan, Blate *et al.* (1998) found that virtually all seeds that were removed while being monitored could be attributed to seed predators and were most likely destroyed; (2) predation by insects; (3) seed germination. Levels of vertebrate predation and removal in the first week were tested, as this was the period of most activity. By removing seeds, vertebrates changed the characteristics of the scats. Thus, the scat remains in later weeks cannot be expected to offer an identical reward to that initially. However, variable (3) seed germination, essentially tests the influence of all types of predation in the weeks until the seed germinated, to determine whether any original scat characteristic had a long-term influence on seed fate.

Logistic regression allows a binomial dependent variable (e.g., killed by insects and not killed by insects) associated with a count variable (in this case the number of seeds killed and not killed by insects in each scat), to be regressed against various independent variables. A linear relationship is not assumed in the test. I identified nine scat characteristics or external factors that may influence the likelihood of seeds escaping predation and germinating. Five of these refer to the content of the scat: (1) seed number; (2) number of seed species; (3) scat weight; (4) seed load (seeds/scat weight); (5) daily rainfall at time of deposition, and two factors relate to the location of the scat: (6) scat density (in 0.25 ha); (7) distance to nearest fruiting tree. The last two factors are temporal variables describing the monthly abundance of alternative foods; (8) ripe fig density (figs ha^{-1}); (9) non-fig fruit abundance (trees ha^{-1}).

The ability of seed predators to locate scats and the chances of a seed germinating may be influenced by scat size (measured by seed number and scat weight), scat density, distance to nearest fruiting tree (since animals may preferentially forage under fruiting trees and, consequently, may be more likely to encounter defecated seeds; this may also influence the ability of seeds to germinate given increased competition from other seedlings under fruiting trees), seed load (this gives an indication of the non-seed faecal component in the scat) and rainfall (which may wash away the faecal attractant and enhance germination). The actual likelihood of seeds being consumed in scats may be influenced by seed load, number of species, seed number, and availability of alternative food sources. Distance of seeds to nearest conspecific tree was not tested for two reasons. First, gibbons defecated only 5.6% of dispersed seeds under parent trees (compared with 28% under fruiting trees in general) and second, a single scat usually contained seeds of several species making a general comparison difficult.

Since monitoring of scats was done over a wide time frame it is possible that a temporal effect – independent of the above variables – may also be influencing seed fate. Indeed, seed fate differed according to the month of deposition for vertebrate predation/removal (ANOVA, $F = 2.6$, $P = 0.01$), insect predation ($F = 8.8$, $P < 0.001$) and seed germination ($F = 3.7$, $P < 0.001$). To account for this variation the data for vertebrates and seed germination were split into two datasets according to whether scats were deposited in months of peak or non-peak vertebrate activity. Further tests indicated no significant temporal variation within these datasets (ANOVA, vertebrates, non-peak, $F = 0.75$, $P = 0.73$, peak, $F = 1.75$, $P = 0.14$; seed germination, non-peak, $F = 0.99$, $P = 0.42$, peak, $F = 0.40$, $P = 0.86$). Most insect predation occurred within 2 mo and the small sample sizes prevented further splitting this data; hence the association between insect predation and scat characteristics could not be tested further. However, when testing for an influence of the two temporal variables (fig and non-fig fruit abundance) entire datasets were used for all three dependent variables.

Each independent variable was tested separately with each dependent variable and its significance determined using the maximum likelihood test, which generates chi-squared values. I also tested all two-way interactions between the significant variables. The main problem with the data set is the obvious lack of independence. The chance of each seed being found in the scat is obviously dependent on whether the other seeds are also found. Thus, care should be taken to view the P-values in terms of their magnitude, rather than the precise value generated (B. Dawkins pers. comm.).

RESULTS

The primary seed shadow generated by gibbons was significantly modified by post-dispersal processes; only 166 seeds (11.3% of monitored seeds) from at least 27 species (50%), and in 57 scats (31%) germinated. Of the 183 scats that were returned to the forest and monitored, all but one were visited by post-dispersal seed predators (indicated by at least one seed being destroyed or removed) and 88.3% of seeds were destroyed. No other causes of seed death were apparent as almost all seeds left untouched by post-dispersal seed predators germinated (only six seeds, 0.4%, did not germinate); hence, post-dispersal predation appeared to be the most prevalent negative influence on seed germination.

Vertebrates destroyed 59 seeds in situ and a further 1206 seeds were removed (86.1% of all seeds in total).

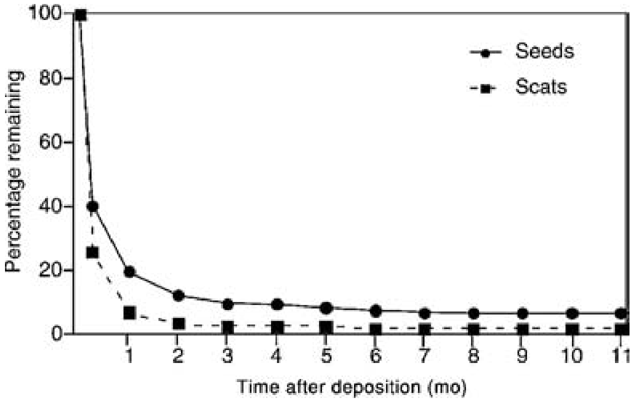

Figure 1. Rate of location of scats and seed removal/predation by vertebrates. Graph shows number of scats or seeds remaining over the study period. Percentages are adjusted to reflect variable monitoring periods (4–11 mo).

Vertebrates visited 180 (98%) of the scats that were returned to the forest. Most scats (74.3%) were located in the first week, and after 5 wk only 7.1% of the scats remained unlocated (Figure 1). Seed removal and predation followed a similar pattern with 59.9% of seeds destroyed or removed in the first week and little additional activity after 13 wk. Dung beetles buried at least 17 seeds (1.2% of seeds) from four species. Other insects killed 33 seeds (2.2% of seeds in 12% of scats) from 11 species. Most insect predation was apparent after 1–2 mo (83.3%), with none occurring after 4 mo of the seeds being deposited in the forest.

Most seeds killed by insects were from scats deposited in the 2 months (March–April) of peak ripe fig availability (Table 1, Figure 2). During these months 8.5% of 225 seeds (30.6% of 41 scats) deposited during that time were killed by insects, compared with 1.5% of 1245 seeds (6.5% of 142 scats) deposited during the remaining months. Due to low sample sizes if the data were split between peaks and non-peaks of insect activity, no further tests were done.

The abundance of alternative food sources in the month of deposition had the strongest influence on vertebrate removal/predation and seed germination (Table 1). Vertebrates usually removed or destroyed more seeds when less alternative foods (non-fig fruit) were available, the exception being in the month fruit abundance was highest, when vertebrate activity also increased (Figure 2). This effect was still significant when considering the actual likelihood of seeds germinating in a scat (Table 1), but highest numbers of germinating seeds came from scats deposited in intermediate periods of fruit abundance (Figure 2).

Only one scat content variable, number of species, influenced vertebrate seed predation/removal and this was prevalent through to seed germination (Table 1). Vertebrates killed proportionally more seeds when more species were present, during peak periods only, while in both peak and non-peak periods seeds were more likely to germinate in scats with few species (Figure 3). The two factors defining scat location influenced seed predation/removal by vertebrates, but neither influenced seed germination (Table 1). Vertebrates tended to remove or kill more seeds when scat density was high (non-peak periods only, Figure 4), or when scats were deposited away from fruiting trees (both periods, Figure 5). No interactions between variables were significant.

DISCUSSION

Post-dispersal events caused a profound change in the primary seed shadow generated by gibbons. Few seeds escaped the attentions of, primarily vertebrate, seed predators and consequently the spatial distribution of the primary seed shadow (clumped) and germinating seeds (random) was different (McConkey 2000). Moreover, only two scat characteristics actually had a significant influence on the chances of seeds germinating and hence, the spatial and physical characteristics of the seed shadow

Table 1. The effects of nine physical and spatial characteristics of 183 gibbon scats on seed fate (killed/removed by vertebrates, killed by insects, germinated). Variables were tested using logistic regression and χ^2 values are shown (P values: * < 0.05, ** < 0.01, *** < 0.001). Variables 1–7 were tested over two periods (peak and non-peak periods of vertebrate removal/predation) for vertebrate and seed-germination categories. Sample sizes for insect predation were too small for these tests. Entire datasets were used for variables 8 and 9.

Independent variables	Vertebrate predation/ removal (1 wk)		Insect predation (4 mo)	Seed germination	
	Non-peak	Peak		Non-peak	Peak
(1) seed number	1.0	0.6	–	2.8	0.4
(2) number of species	1.5	5.1*	–	8.4**	10.1**
(3) scat weight	0.7	0.9	–	0.4	0.4
(4) seed load	2.5	1.1	–	0.7	2.6
(5) rainfall	0.7	0.6	–	0.4	0.8
(6) scat density	23.5***	0.4	–	1.2	0.9
(7) distance to fruiting tree	4.5**	46.3***	–	0.65	1.1
(8) density of ripe figs	2.3		26.7***	2.4	
(9) density of ripe fruit	24.5***		1.3	47.8***	

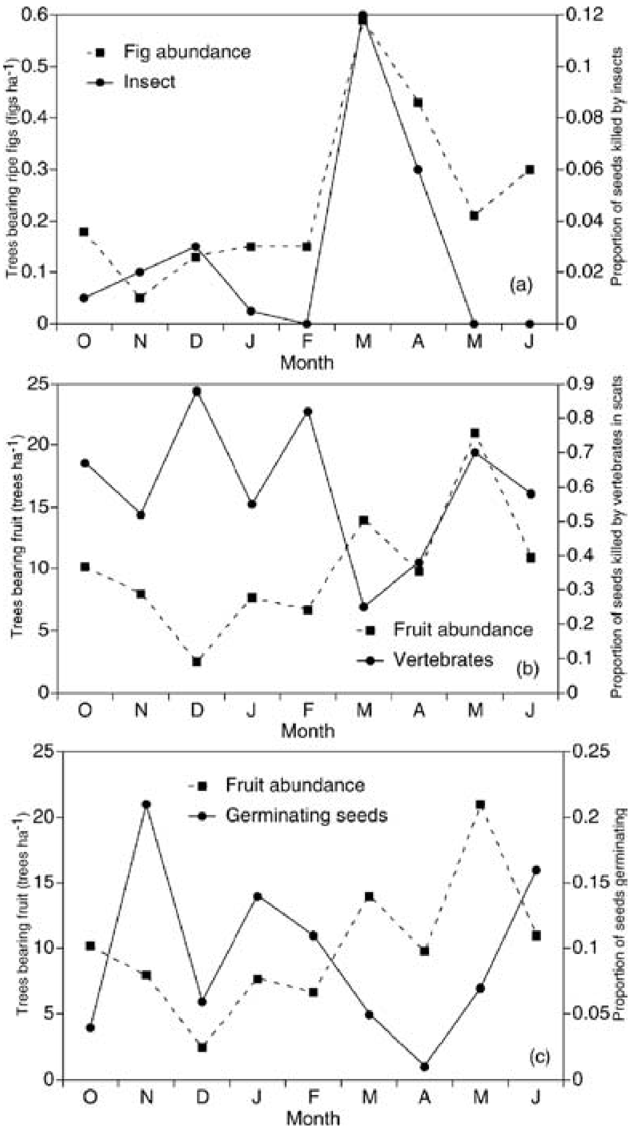

Figure 2. The influence of alternative food source abundance on seed fate: (a) monthly predation by insects in response to ripe fig abundance, (b) monthly removal/predation of seeds by vertebrates in response to non-fig fruit abundance, (c) monthly seed germination in response to non-fig fruit abundance.

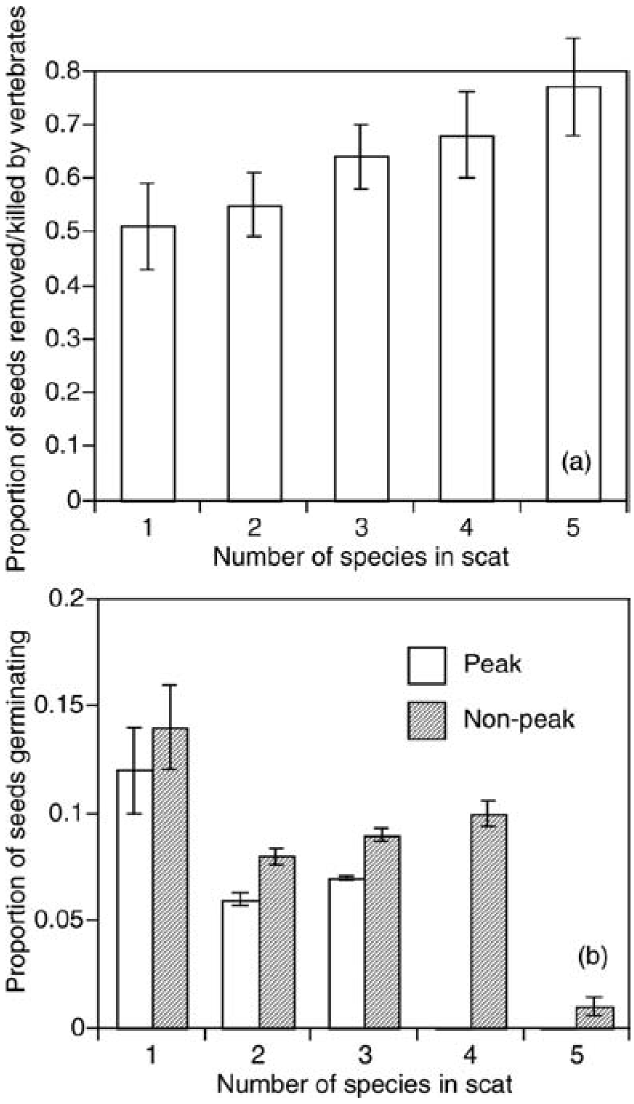

Figure 3. The influence of the number of seed species in scats on: (a) mean proportion and standard error of seeds killed/removed by vertebrates during peak periods of activity, (b) mean proportion and standard error of seeds germinating in scats in both peak and non-peak periods.

gibbons generated had little long-term effect on seed fate. This does not necessarily detract from the importance of gibbons as seed dispersers since primary seed shadows generated by other frugivores may actually generate fewer seedlings; however, these results do indicate that variability between gibbon scats has a minimal influence on early seed fate and one scat is essentially the same as another.

Post-dispersal seed predation by insects and vertebrates is frequently cited as being a major cause of seed mortality in tropical forests (reviewed in Hammond & Brown 1998, Hulme 2002). The high rates of vertebrate seed predation/removal in this study are similar to those reported from other tropical areas, which have included faeces (which is an attractant) in the experiment (Andresen 2002, Chapman 1989). In contrast, insect predation was not an important cause of seed death in defecated seeds at this study site, although the rates found here are still within the range reported in other tropical sites (Hulme 2002). Seedling death is considered a major cause of recruitment limitation in some habitats (Jordano & Herrera 1995, Rey & Alcántara 2000) and is likely to further reduce the number of seeds successfully establishing from gibbon scats.

Although I originally assessed the variables according to whether they may influence the ability of seed predators to find seeds and those that may influence the likelihood of seeds being consumed, virtually all scats were found,

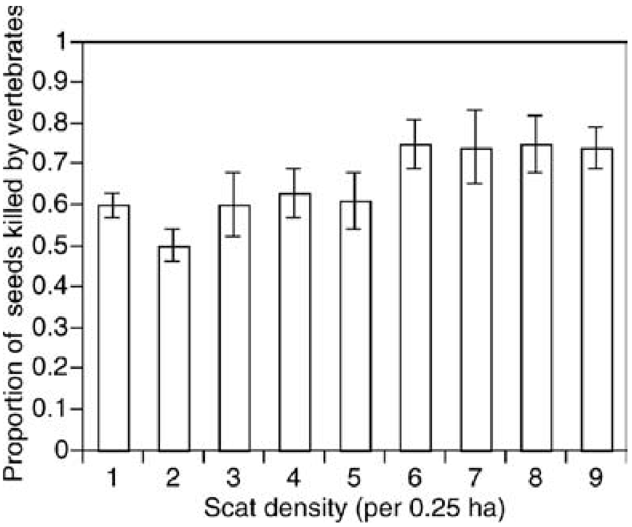

Figure 4. The influence of scat density (mean proportion and standard error shown) on vertebrate predation/removal during the non-peak period of activity.

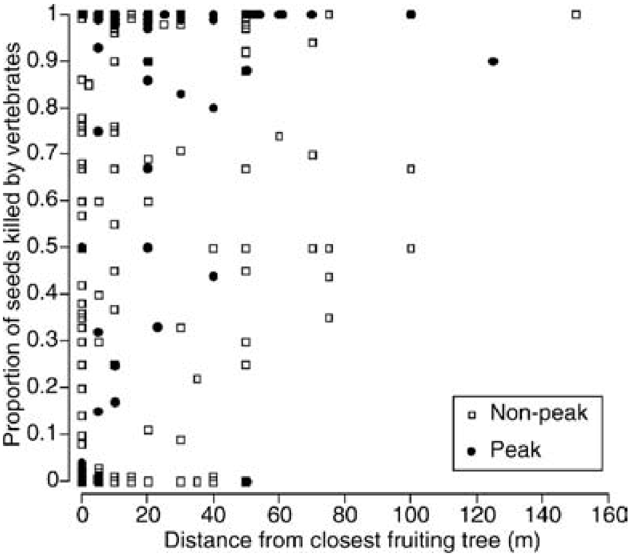

Figure 5. The influence of distance from fruiting tree on vertebrate predation/removal during peak and non-peak periods of activity.

indicating no significant variability in the ability of (at least vertebrate) seed predators to find gibbon scats. Hence, the factors measured influenced the chances of a seed actually being consumed rather than the scat being found. A seed had the highest chance of escaping vertebrate attention if it was dispersed under fruiting trees, in areas that received few scats regularly, in scats with few species and in second yearly fruiting peaks. To escape insect predation a seed should be dispersed when ripe figs were not abundant. The main requirement for seeds to survive long enough to germinate, however, appeared to be related to non-fig fruit abundance at the time of deposition, with higher rates of germination occurring at intermediate periods of abundance (reflecting both immediate seed predation/removal by vertebrates and probably predation in later months). Gibbons at the study site tended to disperse seeds in scats with several seed species, under fruiting trees or along regular routes of travel (McConkey 2000). The component of fruit in their diet was not related to fig abundance, although non-fig fruit consumption increased during the associated fruiting period (McConkey *et al.* 2003). Hence, while one aspect of gibbon behaviour promoted higher rates of escape from seed predators other behavioural aspects had a neutral or negative influence on seed fate.

Some of the factors that were important influences on seed fate in this study have not been commonly considered in experimental tests of seed fate. Number of species in scats has only rarely been considered to influence seed predation (Loiselle 1990) yet it had an important influence on seed fate through to germination in this study. In addition, while several studies have considered the importance of seed density for vertebrate predation, in terms of numbers of seeds in scats (Alcántara *et al.* 2000, Andresen 2002, Chapman 1989, Forget & Milleron 1991, Lott *et al.* 1995, Sanchéz-Cordero & Martínez-Gallardo 1998), few have considered scat density (Andresen 2002). The response of vertebrates to seed density has been variable, probably due to regional differences (Andresen 2002). In this study, vertebrates responded to scat density, but seed number within scats had no influence.

Many studies consider the influence of distance from parent trees on seed fate. This was not tested in this study due to the few scats that were actually dispersed under conspecifics. However, if a frugivore forages in many tree species and disperses seeds in their scats, more seeds are likely to be dispersed under non-conspecific fruiting trees (McConkey 2000). This factor has also been ignored in previous studies yet it was an important determinant of vertebrate predation/removal in this study. Given a choice, vertebrates clearly preferred clean seeds to those that had passed through the gibbon gut (McConkey 1999), so seeds defecated under fruiting trees (where alternative food is available) usually had a higher chance of escaping seed predation than those at greater distances. However, this influence had become neutral by the time seeds germinated.

Another example of vertebrates preferring alternative food sources to seeds in scats is shown in the relationship with non-fig fruit abundance. When fruit was less abundant vertebrates took more seeds from scats, and when fruit was more abundant they took less. The only exception to this was during the fruiting peak when seed predation/removal also increased. There are three possible explanations for this exception. The most likely cause is the influx of pigs (*Sus barbatus*) into the study area during this period. Pig numbers increased by more than 15-fold (McConkey & Chivers 2004), and almost certainly took more seeds during this time. Alternatively, rodents time their breeding period to coincide with peaks in food abundance (Adler & Beatty 1997, Notman & Gorchov 2001) and the increased population size would naturally put additional demands on food sources. Lastly, increased rates of seed removal may indicate caching by rodents. In the neotropics caching occurs in the periods of high fruit abundance (Forget *et al.* 2002). Some South-East Asian rodents cache seeds (Yasuda *et al.* 2000) and *Maxomys rajah* Thomas was observed caching seeds at the study site (pers. obs.), but little is known of the prevalence of such activities in the region.

There are three problems in this study that may affect the interpretation of results. The study is short-term and it has become apparent that processes can change immensely between years in a tropical forest (Schupp 1990). Hence the factors that seemed important during the study period, may be less so in a longer-term study. The second problem was the inability to distinguish which post-dispersal seed predators were responsible for seed removal or destruction and this prevents some interpretation of the observed trends. Experimental studies indicated rodents were the main post-dispersal seed predator at the study site (McConkey 2005) and both pigs and rats are the primary seed predators at other South-East Asian sites (Blate *et al.* 1998, Curran & Leighton 2000, Ickes *et al.* 2001, Miura *et al.* 1997). Finally, most seeds were removed completely from the deposit site and the fate of these is not known. It is likely that some seeds were cached and a proportion of these may have germinated. Rats frequently remove large numbers of seeds to husking stations (sheltered areas where the predation risk is less) to consume and almost all seeds are destroyed (McConkey *et al.* 2002*b*). Pigs can also remove entire scats with little trace after 1 mo. Although it is not possible to determine the fate of seeds removed in this study, I suggest that most were eaten.

Gibbons are considered important seed dispersers in Asian forests because they disperse most of the species they consume and disperse large quantities of seeds (McConkey 2000), however most seeds dispersed by gibbons are destroyed or removed during post-dispersal stages and variation in the characteristics of the primary seed shadow had little lasting impact on the probability of seeds germinating. There is increasing evidence that plant populations are seed limited (Clark *et al.* 1999), and while the proportion of seeds germinating in this study appears low the rate is not uncommonly low for tropical forests (Chapman 1989, Hulme 1998, Notman & Gorchov 2001). Moreover, the forests of Barito Ulu are fairly depauperate in alternative frugivores capable of dispersing the same plant species as gibbons (McConkey 1999, McConkey & Chivers 2004). Hence, the few seeds dispersed that do reach 'safe sites' may in fact be crucial if recruitment limitation is a problem.

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