

Functional response to fruiting seasonality by a primate seed predator, red leaf monkey (*Presbytis rubicunda*)

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Abstract: The predator satiation hypothesis is one plausible explanation for masting in lowland dipterocarp forests in SE Asia. Hence, evaluation of behavioral patterns of seed predators have the potential to provide support for the predator satiation hypothesis. In order to evaluate possible mechanisms that could result in predator satiation, we studied the functional response in the seed predation behavior to fruiting seasonality of red leaf monkeys (*Presbytis rubicunda* Müller, 1838, Colobinae) in Danum Valley, Sabah, northern Borneo. Specifically, we sought to answer the two questions: (1) when fruit availability increases, to what extent do red leaf monkeys increase their seed eating? and (2) do red leaf monkeys change the degree to which they pursue one species of seeds in response to the changes in community-level fruit availability? In response to the increased fruit availability, red leaf monkeys extended their time spent feeding on seeds as much as 18 fold. This large functional response resulted from the elongated total feeding time and the preference for seeds by red leaf monkeys. Feeding time tended to increase, up to 28 % of the observation time, with increasing fruit availability. In response to increased fruiting seasonality, the monkeys increased the number of species and plant individuals upon whose seeds they depredated. Time spent feeding on seeds per species or individual, or for the most frequently eaten species or individual, was not affected by fruit availability. Similarly, the duration of one seed-feeding event was unaffected by the fruit availability. Hence, while our results demonstrate a functional response to mast fruiting, we found no support for the predator satiation hypothesis. The existence of an abundant alternative resource (young leaves) is one of several likely reasons for the weak persistence toward seeds shown by red leaf monkeys, which is contradictory to the assumption of the predator satiation hypothesis.

Resumen: La hipótesis de la saciedad del depredador es una explicación plausible de la fructificación masiva en bosques de dipterocarpaceas de tierras bajas del sureste de Asia. Por lo tanto, la evaluación de los patrones de comportamiento de los depredadores de semillas podría potencialmente apoyar la hipótesis de saciedad del depredador. Para evaluar los posibles mecanismos que podrían resultar en la saciedad del depredador, estudiamos la respuesta funcional a la estacionalidad de la fructificación en el comportamiento depredador de semillas de los langures marrones (*Presbytis rubicunda* Müller, 1838, Colobinae) en el Valle Danum, Sabah, norte de Borneo. Específicamente, tratamos de responder a estas dos preguntas: (1) cuando aumenta la disponibilidad de fruta, ¿en qué medida los langures marrones incrementan su consumo de semillas?, y (2) cambian los langures marrones el grado en que procuran una especie de semillas en respuesta a los cambios en la disponibilidad de fruta en la comunidad? En respuesta a una mayor disponibilidad de frutos, los langures marrones pasaron más tiempo, hasta 18 veces, alimentándose de semillas. Esta respuesta funcional grande se derivó del alargamiento del tiempo total de alimentación y de la preferencia de los langures marrones por las semillas. El tiempo de alimentación tendió a crecer, hasta 28 % del tiempo de observación,

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con el aumento en la disponibilidad de frutos. Como respuesta al aumento en la estacionalidad de la fructificación aumentaron el número de especies y de plantas individuales de las que se alimentan los monos. El tiempo dedicado a comer semillas por especie o por individuo, o para la especie o individuo consumido más frecuentemente, no se vio afectado por la disponibilidad de fruta. De forma similar, la duración de un evento de consumo de semillas no fue afectado por la disponibilidad de fruta. Por lo tanto, Si bien nuestros resultados demuestran que hay una respuesta funcional a la fructificación masiva, no apoyan la hipótesis de saciedad del depredador. La existencia de un recurso alternativo abundante (hojas jóvenes) es una de las varias razones posibles de la persistencia débil hacia las semillas que mostraron los langures marrones, lo cual contradice el supuesto de la hipótesis de saciedad del depredador.

Resumo: A hipótese da saciedade do predador é uma explicação plausível para a frutificação maciça em florestas de dipterocarpaceas nas terras de várzea no Sudeste da Ásia. Por isso, a avaliação de padrões de comportamento dos predadores de sementes poderia potencialmente suportar a hipótese de saciedade do predador. A fim de avaliar os possíveis mecanismos que poderiam resultar na saciedade do predador, foi estudada a resposta funcional da sazonalidade da frutificação no comportamento depredador de sementes dos langures vermelhos (*Presbytis rubicunda* Müller, 1838, Colobinae) no Danum Valley, Sabah, no norte de Bornéu. Especificamente, procurou-se responder a duas perguntas: (1) quando aumenta a disponibilidade de fruta, até que ponto os langures vermelhos aumentam o seu consumo de sementes? e (2) os langures vermelhos alteram o grau em que buscam uma espécie de sementes, em resposta às mudanças no nível, disponibilidade de frutos na comunidade? Em resposta ao aumento da disponibilidade de frutos, os langures vermelhos passaram mais tempo, até 18 vezes, alimentando-se de sementes. Esta resposta funcional grande resultou do alargamento do tempo total de alimentação e da preferência dos langures vermelhos para as sementes. O tempo de alimentação tendeu a aumentar, até 28% do tempo de observação, com o aumento da disponibilidade de frutos. Em resposta ao aumento da sazonalidade da frutificação, aumentaram o número de espécies e plantas individuais de que se alimentam os langures. O tempo despendido a alimentar-se de sementes por espécie ou por individuo, ou para a espécie ou individuo consumido mais frequentemente, não foi afetado pela disponibilidade de frutos. Da mesma forma, a duração de um evento de consumo de sementes não foi afetada pela disponibilidade de fruta. Assim, enquanto os nossos resultados demonstram haver uma resposta funcional à frutificação massiva, não apoiam a hipótese de saciedade de predador. A existência de um recurso alternativo abundante (folhas jovens) é uma das várias razões prováveis para a fraca persistência para sementes mostrada pelos langures vermelhos, o que contradiz a hipótese de saciedade do predador.

Key words: Diet, functional response, mast fruiting, predator satiation hypothesis, *Presbytis rubicunda*, seed.

Introduction

The degree of inter-individual or inter-species synchronization of plant reproduction varies over time (Herrera *et al.* 1998). When many individuals or species of plants reproduce synchronously, the result is often called masting. It occurs in many taxa, from tropical to boreal regions (Herrera *et al.* 1998; Newbery *et al.* 2006; Rossi *et al.* 2012; Schauber *et al.* 2002). Several hypotheses have been proposed to explain the evolution of mast

fruiting (Kelly 1994). For example, pollination is facilitated by synchronous flowering, in particular for wind-pollinated plants (Rossi *et al.* 2012). Masting may also be a response to environmental fluctuations (Newbery *et al.* 2006). One often examined hypothesis is the predator satiation hypothesis (Janzen 1974), which assumes that various species or individuals of plants can escape seed predation by synchronizing fruiting to produce a large amount of seeds, which exceeds the capacity of seed predators to consume them all.

Lowland dipterocarp forests in Southeast Asia including the Malay Peninsula, Borneo and Sumatra are well known for their community-level general flowering and subsequent mast fruiting. In these lowland forests, many plants flower for a few weeks to a few months at the same time and subsequently yield a large amount of fruit massively (Sakai 2002; Wich & van Schaik 2000). Both plants of Dipterocarpaceae (dominant family) and other families often have synchronous flowering and mast fruiting. These synchronous events occur at multiyear and unpredictable intervals, typically of 2 - 6 years (Sakai 2002). Because wind pollination is rare and there is little seasonality in climate, past studies on the ultimate cause of masting have concentrated on predator satiation, the most plausible explanation for masting in this region.

Past studies on predator satiation in Southeast Asia have been conducted primarily through plant-based data, such as collection of seed samples or focal observation of fruiting trees. These plant-based studies compared the proportion of depredated seeds in and out of, or by the intensity of, mast fruiting. Data have been accumulated in particular for dipterocarps, the most dominant family in this region's forests. For example, Sun *et al.* (2007) studied predation on dipterocarp seeds for three mast fruiting events in Pasoh, Peninsular Malaysia and found that the proportion of surviving seeds was largest during the largest mast fruiting event, which is in accordance with the predator satiation hypothesis. Similarly, Curran & Leighton (2000) studied seed predation on dipterocarps for > 8 years in the Gunung Palung National Park, West Kalimantan and found that during the large-scale mast fruiting, the proportion of depredated seeds decreased because (1) resident predators fed mainly on non-dipterocarp seeds and (2) migrant predators arrived after the peak of fruiting, allowing most dipterocarp seeds to escape predation.

Animal-based data, particularly data on the diet of a seed predator species for a prolonged period, provide another perspective which can complement plant-based data. An animal-based approach may directly answer the question of why and how animals change their seed predation rates as there are a number of factors which limit animals' feeding behavior, such as foraging time and gut capacity. Seed predation by animals is affected not only by seed availability but also by these physiological limitations, which cannot be studied using a plant-based approach. Therefore,

animal-based approach can reveal mechanism related to predator satiation.

Primates play indispensable roles as seed dispersers in tropical forests and some forests appear unable to regenerate, or species composition is considerably altered, if they are absent on a long-term basis (Chapman & Onderdonk 1998; Kitamura *et al.* 2002; Nuñez-Iturri & Howe 2007). Primates are also important as seed predators (Sun *et al.* 2007), such as in the lowland dipterocarp forest of Pasoh where leaf monkeys (*Presbytis* spp.) are the major cause of seed mortality. In fact, leaf monkeys constitute 39 % of the pre-dispersal seed mortality, which is larger than any other causes such as beetle and rodent predation or fungal infection (Sun *et al.* 2007). Because the biomass of primates in Pasoh is similar to other Southeast Asian forests (Gupta & Chivers 1999), primates in other regions of Southeast Asia are likely to impose a similar degree of predation pressure on seeds.

Predator satiation has been extensively tested among species which increase their number through migration or fast reproduction, such as rodents and insects (Hosaka *et al.* 2009; Nakagawa *et al.* 2005). However, such a numerical response is rare among primates, except for migration of Sumatran orangutan (*Pongo abelii*) (Buij *et al.* 2002), as most primates respond to fruit masting via a functional response, such as a dietary shift (Hemingway & Bynum 2005), which is found among Bornean primates (Harrison *et al.* 2010; Kanamori *et al.* 2010; Vogel *et al.* 2009). However, because gut capacity and foraging time are limited, animals cannot infinitely increase their seed predation rates when they do not increase their number. As a result, the relationship between the proportion of seeds predated and seed availability is hyperbolic (Fletcher *et al.* 2010; Ruscoe *et al.* 2005). This relationship suggests that if the amount of seeds exceeds the amount that primates can consume, predator satiation could occur.

We studied the functional response to seasonal changes in fruit availability by the red leaf monkey (*Presbytis rubicunda*), a seed predator of the Bornean forest (Davies & Baillie 1988; Davies 1991; Supriatna *et al.* 1986). Red leaf monkeys prefer seeds but will switch their main food to young leaves when fruit availability decreases (Hanya & Bernard 2012). Given the red leaf monkeys' preference for seeds, we sought to answer two basic questions about functional responses: (1) when fruit availability increases, to what extent do red leaf monkeys increase their seed eating; and,

(2) do red leaf monkeys change the degree to which they pursue one species of seeds in response to the changes in community-level fruit availability? The answers to both of these questions can yield insights into predator satiation. Specifically, if red leaf monkeys cannot increase their seed consumption with increasing fruit availability, this would suggest satiation. Likewise, when fruit availability is low, seeds are less likely to escape predation. If the monkeys keep trying to eat seeds even when the overall fruit availability decreases, they may persist on one species and/or increase the seed-feeding time per species or per individual plant.

Material and methods

Study site

We conducted our study in the primary forest surrounding the Danum Valley Field Centre (DVFC) (4° 57' N, 117° 48' E, 300 m asl) within the Danum Valley Conservation Area (438 km²) in eastern Sabah, northern Borneo during from December 2006 to December 2008. During the study period rainfall was 3,115 mm yr⁻¹, and average daily maximum, minimum and mean temperatures were 31.4 °C, 22.5 °C and 26.9 °C, respectively. The forest was predominantly composed of lowland dipterocarp trees with canopy height of approximately 50 m. Biomass of leaf monkeys was 354 kg km⁻² (Hanya & Bernard, unpublished data), which is smaller than that in Pasoh (541 kg km⁻²) (Gupta & Chivers 1999), where leaf monkeys are known to be significant seed predators.

Behavioral observation

To answer our main questions, we examine the following behavioral responses by red leaf monkeys to community-level seasonal fluctuations in fruiting: (1) total feeding time, (2) feeding time on seeds, (3) number of species whose seeds are eaten, (4) number of individuals whose seeds are eaten, (5) average feeding time spent on seeds per species, (6) average feeding time on seeds per individual plant, (7) feeding time on seeds for the most frequently eaten species, (8) feeding time on seeds for the most frequently eaten individual plants, and (9) duration of one seed-feeding event. The first question is examined by data (1) and (2). The second question is examined by data (5)-(9), with data (3) and (4) providing necessary background information for them. We examined both average feeding time and feeding time on the most frequently eaten species/individuals. This is be-

cause the former indicates the overall tendency in the effect imposed on each species/individual while the latter represents how strongly monkeys persist on one particular species/individual. As an index of the intensity of seed predation, we used the proportion of feeding time on seeds and whole fruits to the total observation time of red leaf monkeys (seed-predation time, hereafter) for data (5)-(8). Feeding time is widely accepted as an index of dietary composition in wild primate studies (Hohmann *et al.* 2006), and it is suitable for measuring how animals allocate time, one of their most limited resources (Dunbar 1996; Hanya 2004b), to each species or individual.

The study subjects were a habituated group of red leaf monkeys of 8 - 12 individuals, including 0 - 4 infants that were born during the study period. They were observed from around 6:00 until 16:00 for five to ten days per month. The monkeys' behavior was recorded by scan sampling: every 10 min, their activity (feeding, moving, or resting) was recorded for all visible individuals, except for dependent infants. When they were feeding, we recorded the food category (young leaves, seeds, whole fruits, flowers, bark, pith and other foods), marked the tree with a numbered tape, and collected samples (both leaves and fruits) for later identification. When the monkeys ate whole fruits, they were always unripe, and we neither observed them spitting out seeds nor detected any seeds in their faeces. Therefore, both seed-eating and whole fruit-eating seemed to function as seed predation. Plant identification was done by a trained staff member at the DVFC using reference specimens at the DVFC herbarium. Although it was often difficult to identify samples to the species level due to the incomplete state of samples, we could identify them to the genus level in almost all cases. Consequently, the number of eaten species was a conservative estimate. However, we assume that it roughly reflected the actual number of species, since most foods belonged to different genera. Over the 25 month study period we observed the monkeys for 1,141 h, with monthly observation times ranging from 16 to 87 h (mean: 46 h). Observation time per day was 7.2 ± 2.3 (SD) h. Sometimes we could not find monkeys in the early morning or terminated observation before 16:00 due to heavy rain.

Phenology

Fruiting activities of trees of ≥ 10 cm dbh were monitored monthly since July 2004 by the DVFC,

using the same plot set by Norhayati (2001) and the same protocol used in the census conducted from August 1997 to December 2000 (Wong *et al.* 2005). Five transects, each 20×100 m, were established in a primary forest within the home range of the subject group. The transects were placed every 400 m along the 2-km trail. Trees with ≥ 10 cm dbh inside the transects were tagged, numbered and identified to species level when possible. Total number of monitored stems in the five transects was 511 - 533, changing due to the death of monitored stems. We included only the genera that were actually eaten by leaf monkeys in the analysis. The exclusion of non-food species did not affect the results significantly because food and total fruiting trees positively correlated significantly ($r = 0.97$, $P < 0.0001$). Both ripe and unripe foods were included because red leaf monkeys ate both.

Data analysis

Seed-predation time was calculated as follows. Due to the high canopy and dense vegetation, the number of individuals seen in each scan was low (mean: 1.95, SD: 1.12). In order to avoid overrepresentation of highly visible behaviors or foods, the gross sum of a scan was not used to calculate the dietary composition. Rather, for each scan, we divided the number of animals engaged in each activity (in the case of feeding, the number of individuals feeding on the particular food) by the total number of animals recorded in the scan (Agetsuma 1995; Harrison 1985; Maruhashi 1981). This value was summed for all of the seed and whole-fruit eating (both ripe and unripe) for each species/plant individual for each month and divided by the total number of scans in the month, thus indicating the proportion of time spent feeding for that species/plant individual of seeds during the observation time in that month. We only used the data from the first 40 hours of monthly observations for the analysis since the number of plant species eaten is dependent on the duration of observation time. We excluded five months of observations (December 2006, January and August 2007, and June and December 2008) because we had < 40 hours of observations in those months.

The average duration of one seed-feeding event was defined as the number of scans in which at least one individual monkey was observed to eat the seeds of a plant individual. If all of the monkeys left the feeding tree, the event was

regarded as having stopped, where as if they began feeding afterwards, it was regarded as a different event. Strictly speaking, the duration of one feeding event cannot be recorded by systematic focal-tree observation (Vogel & Janson 2007). However, we assume that our definition can be used as a proxy for it, since the group spread was rather small (< 50 m) and seed-feeding was a conspicuous behavior (monkeys dropped fruits onto the ground) and thus unlikely to be overlooked.

Using a generalized linear model (GLM), we investigated the effect of monthly fruiting phenology on (1) total feeding time, (2) feeding time on seeds, (5) average feeding time spent on seeds per species, (6) average feeding time on seeds per individual plant, (7) feeding time on seeds for the most frequently eaten species, (8) feeding time on seeds for the most frequently eaten individual plants, and (9) duration of one seed-feeding event. As an independent variable, we examined a null model (a model with only constant), a model including the proportion of fruiting trees, and a model including values of both the proportion of fruiting trees and its square. We selected the best-fit model among these three using Akaike's Information Criterion corrected for small samples (AICc) (Burnham & Anderson 2002). Dependent variables were normally distributed according to the Kolmogorov - Smirnov test ($P > 0.1$). Because (3) number of species whose seeds are eaten and (4) number of individuals whose seeds are eaten, (count data) did not fit the Poisson distribution (Kolmogorov-Smirnov test, $P = 0.032$ and 0.0002 , respectively), we examined the effect of fruiting seasonality on these factors by the nonparametric Spearman's rank correlation. We used R 2.13.2. (© 2011 The R Foundation for Statistical Computing) for all of the statistical analyses.

Results

Over the 25 months study period there was one clear peak of fruiting from May through October 2007 (Fig. 1), for both food trees and the entire plant community. This peak in fruiting was the largest mast recorded between July 2004 and December 2008, as well as when compared to an earlier time period of August 1997 until December 2000 (Wong *et al.* 2005). During this peak, 2.8 % to 6.7 % of trees bore fruit compared to 0 % to 1.9 % of trees outside of this masting period. Fruiting of dipterocarps was not observed during our study period in 2006 - 2008, but they were observed to bear fruit in 2005.

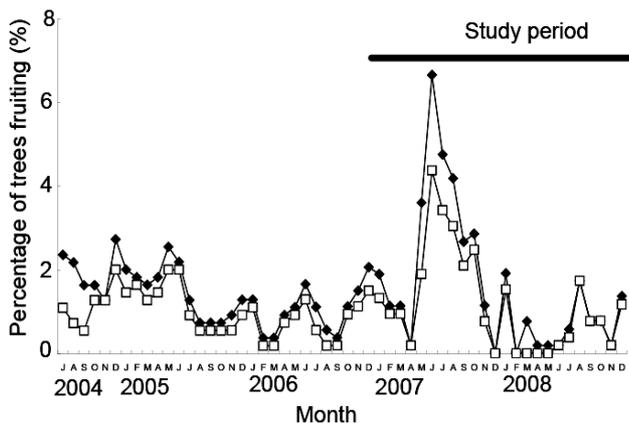


Fig. 1. Percentage of trees fruiting (including both ripe and unripe) between July 2004 and December 2008 for all the monitored trees (closed diamond) and only species eaten by red leaf monkey (open square).

Red leaf monkeys ate both seeds (54 species) and whole fruits (27 species) of at least 65 species, which were identified to at least the genus level. For some species, both seed-feeding (accompanied with pulp discarding behavior) and whole fruit-feeding were observed. These species included in the families of Oleaceae, Lauraceae, Myrtaceae, Fagaceae, Sapindaceae, Moraceae, Leguminosae, Meliaceae, Myrsinaceae, and Euphorbiaceae, but they did not include species of Dipterocarpaceae. When fruit availability decreased, the monkeys ate more young leaves, in particular a liana species (*Spatholobus macropterus*, Leguminosae), which constituted 28 % of the total feeding time (Hanya & Bernard 2012).

Red leaf monkeys increased their time consuming seeds (Fig. 2a, Table 1a) and their total feeding time (Fig. 2b, Table 1b) in response to the increased fruit availability. For the time spent consuming seeds, the best fit model included the square of the fruit availability (Table 1a). However, in the range of the current data set, time spent on seed consumption increased almost monotonously with increasing fruit availability (Fig. 2a). Maximum feeding time was 28 % of the observation time, which is 2.9 times the lowest value (9.7 %, July 2008). The time spent consuming seeds was 18 times greater during the highest (July 2007, 22 %) month compared to the lowest (February 2008, 1.2 %) month. Monthly fruit availability and the number of species or individual plants whose seeds were depredated by red leaf monkeys were positively correlated (species: $r = 0.57$, $P = 0.009$; plant individuals: $r = 0.46$, $P = 0.039$; Fig. 3). On the other hand, there

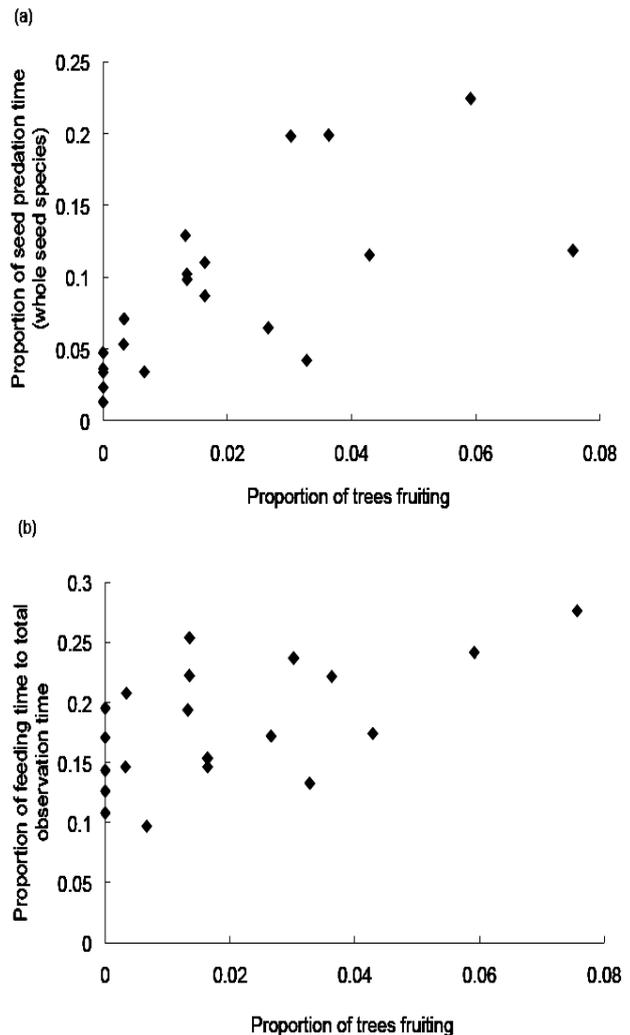


Fig. 2. The proportion of trees producing fruit eaten by red leaf monkeys in relation to (a) the proportion of time spent feeding on seeds and whole fruits and, (b) the proportion of total feeding time to total observation time of red leaf monkeys.

were no relationships between monthly fruit availability and the time spent depredating seeds per species or per individual plant (Fig. 4). Null models were the best-fit models for both cases (Table 2). When the fruiting was highest (May through October 2007), seed-predation time per species or individual was intermediate. Outside of these six months, seed-predation time per species or individual was variable. Seed-predation time for the most frequently eaten species or plant individuals tended to be long in the months when fruit availability was high (Fig. 5, Table 3). Average duration of seed - feeding events was not affected by the fruit availability of the month (Fig. 6; Table 4).

Table 1. Generalized linear model on the effect of fruiting seasonality on proportion of (a) feeding time spent on seed and whole fruit feeding and (b) total feeding time to the observation time of red leaf monkeys.

(a) Effect on the proportion of feeding time spent on seed and whole fruit feeding

Intercept	Coefficient		R ²	-2LL	K	AIC	AICc	ΔAICc	w _i	p	
	#Trees fruiting	#Trees fruiting ²								#Trees fruiting	#Trees fruiting ²
0.09	-	-	-	-52	0	-52	-52	12	0.00	-	-
0.05	1.94	-	0.45	-60	1	-62	-61.8	2.2	0.25	0.0011	-
0.03	4.56	-41.26	0.52	-60.7	2	-64.7	-64	0	0.75	0.0031	0.0492

(b) Effect on the proportion of total feeding time

0.18	-	-	-	-59.8	0	-59.8	-59.8	6.2	0.03	-	-
0.15	1.39	-	0.34	-64.2	1	-66.2	-66.2	0	0.75	0.0065	-
0.16	0.95	6.86	0.27	-60.4	2	-64.4	-64.4	2.3	0.24	0.4850	0.7310

R²: the proportion of variations explained in this model, -2LL: -2*Log likelihood, K: number of parameters, AIC: Akaike's Information Criterion (indicator of model fitness), AICc: corrected AIC for small sample size (AIC=AICc for null model), ΔAICc= difference in AICc with the best-fit model, w_i: Akaike weight. **Bold** indicates the best-fit model.

Table 2. Generalized linear model on the effect of fruiting seasonality on seed-predation time (a) per species and (b) per individual plant.

(a) Seed predation time per species

Intercept	Coefficient		R ²	-2LL	K	AIC	AICc	ΔAICc	w _i	p	
	#Trees fruiting	#Trees fruiting ²								#Trees fruiting	#Trees fruiting ²
0.02	-	-	-	-136.8	0	-136.8	-136.8	0	0.66	-	-
0.02	0.04	-	-0.04	-133.1	1	-135.1	-134.9	1.9	0.26	0.6190	-
0.02	0.14	-1.60	-0.089	-129.3	2	-133.3	-132.6	4.2	0.08	0.5570	0.6550

(b) Seed predation time per individual plant

0.01	-	-	-	-138.2	0	-138.2	-138.2	0	0.66	-	-
0.01	0.06	-	-0.025	-134.8	1	-136.8	-136.6	1.6	0.30	0.4733	-
0.01	0.15	-1.48	-0.073	-131	2	-135	-134.3	3.9	0.09	0.5173	0.6652

Discussion

When the fruit availability increases, to what extent can red leaf monkeys increase the amount of seed predation?

Red leaf monkeys increased their total seed predation time with the increased fruit availability (Table 5). The time spent on seed predation increased by as much as 18 fold, which is greater than reported for dipterocarp seeds predation by leaf monkeys in Pasoh that had an eight fold increase (Sun *et al.* 2007). This large functional response results from the elongated total feeding

time in response to increased fruit availability and the preference on seeds by red leaf monkeys. That is, when seed availability increased, red leaf monkeys prolonged their total feeding time - namely their feeding effort - suggesting that they adopt a strategy to maximize their food intake. The maximum feeding time was 28 % of the observation time, which was recorded during the highly fruiting period of June 2007. It remains unclear whether red leaf monkeys can elongate feeding time beyond this level as it is usual for leaf monkeys to extend their monthly feeding time to around 30 % (Li & Rogers 2004; Matsuda *et al.* 2009; Zhou *et al.* 2007), or even to more than 40 %

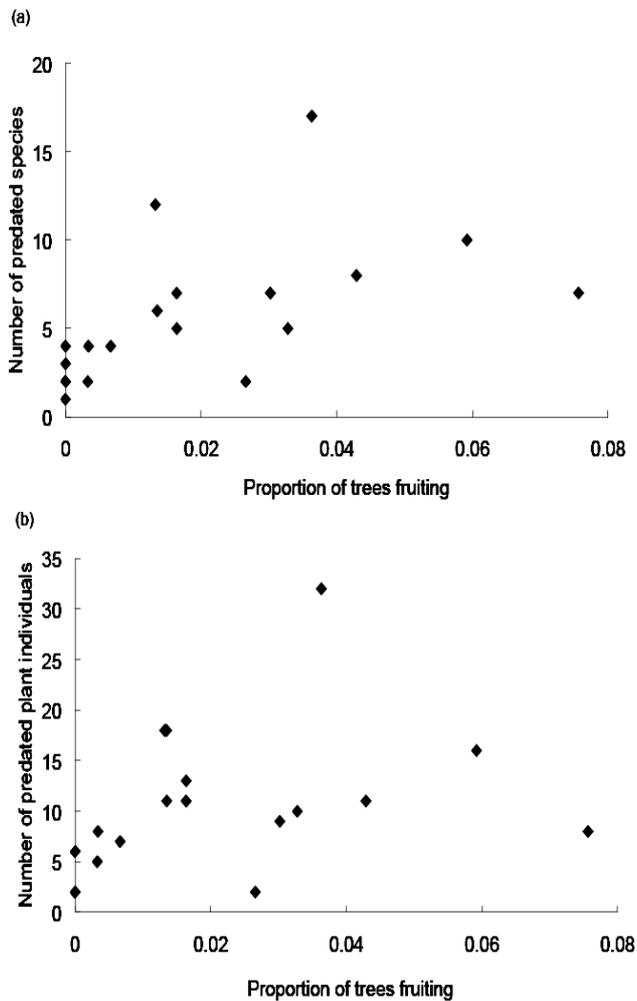


Fig. 3. The proportion of trees producing fruit eaten by red leaf monkeys in relation to the (a) number of species and (b) number of plant individuals from which seeds were depredated by red leaf monkeys.

(Fashing *et al.* 2007; Newton 1992). If the red leaf monkey's gut capacity reached the maximum at the fruiting peak observed in our study, predator satiation could occur when an even larger mast fruiting occurs.

Seeds and young leaves are the two main foods of leaf monkeys (Kirkpatrick 1999), including the study population (Hanya & Bernard 2012), with the literature indicating variability in their preference for seeds or young leaves (Dasilva 1994; Zhou *et al.* 2009). In Danum Valley, the availability of fruiting trees is more limited than that of flushing trees (mean proportion of fruiting trees: 1.5, SD: 1.2 % vs. mean proportion of flushing trees: 12.9, SD: 7.9 %; data provided by the Danum Valley Field Centre, 54 months between 2004 and 2008). An analysis of seasonal

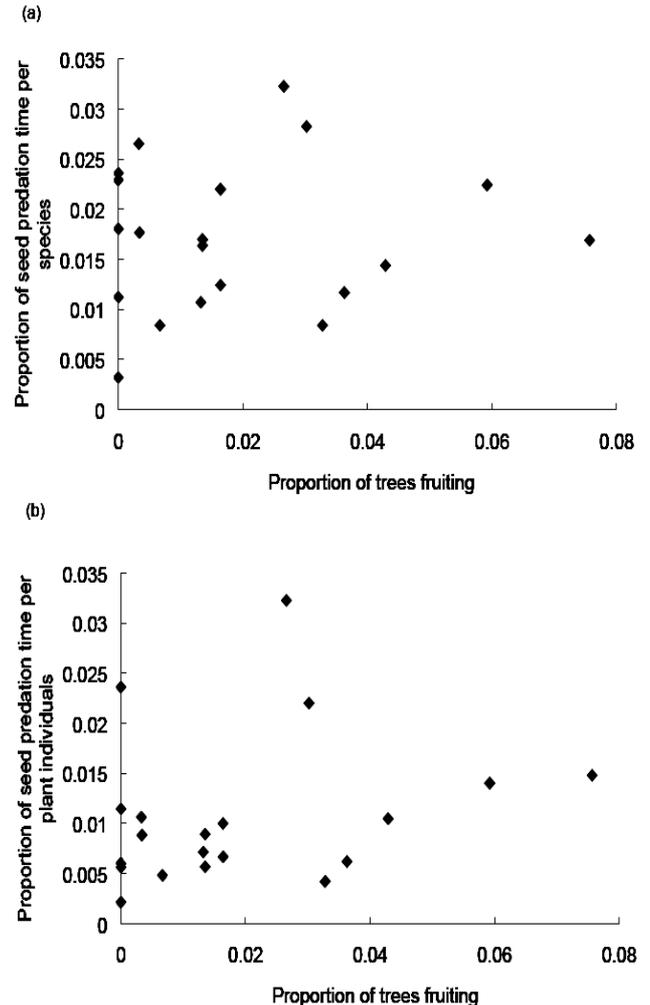


Fig. 4. The proportion of trees producing fruit eaten by red leaf monkeys in relation to the proportion of time spent feeding on seeds and whole fruits divided by the number of (a) plant species or (b) plant individuals.

change in dietary composition and phenology indicates that when fruit was abundant, red leaf monkeys ate more seeds and less young leaves. However, flushing phenology did not result in any diet change (Hanya & Bernard 2012), suggesting that red leaf monkeys prefer seeds over young leaves. In fact, red leaf monkeys concentrated on the more limited resources (seeds) whenever they were available.

Red leaf monkeys also increased the number of seed species they depredated in response to the increased fruit availability. Because seeds contain secondary compounds to protect themselves from predators (Janzen 1971), it may be beneficial for red leaf monkeys to reduce the intake of a particular species and switch to a different species in

Table 3. Generalized linear model on the effect of fruiting seasonality on the feeding time on most frequently eaten (a) seed species and (b) plant individuals.

(a) Most frequently eaten species											
Intercept	Coefficient		R ²	-2LL	K	AIC	AICc	ΔAICc	w _i	p	
	#Trees fruiting	#Trees fruiting ²								#Trees fruiting	#Trees fruiting ²
0.04	-	-	-	-90.4	0	-90.4	-90.4	2.1	0.18	-	-
0.03	0.49	-	0.15	-90.7	1	-92.7	-92.5	0	0.53	0.0518	-
0.03	1.14	-10.35	0.15	-88	2	-92	-91.3	1.2	0.29	0.1058	0.3089

(b) Most frequently eaten plant individuals											
Intercept	Coefficient		R ²	-2LL	K	AIC	AICc	ΔAICc	w _i	p	
	#Trees fruiting	#Trees fruiting ²								#Trees fruiting	#Trees fruiting ²
0.03	-	-	-	-52	0	-86.1	-86.1	1.3	0.27	-	-
0.02	0.49	-	0.112	-85.6	1	-87.6	-87.4	0	0.53	0.0819	-
0.02	1.36	-13.71	0.14	-83.3	2	-87.3	-86.6	0.8	0.35	0.0882	0.2328

Table 4. Generalized linear model on the effect of fruiting seasonality on average duration of seed-feeding event in the month.

Intercept	Coefficient		R ²	-2LL	K	AIC	AICc	ΔAICc	w _i	p	
	#Trees fruiting	#Trees fruiting ²								#Trees fruiting	#Trees fruiting ²
3.01	-	-	-	74.5	0	74.5	74.5	0	0.58	-	-
2.72	14.72	-	-0.006	77.6	1	75.6	75.8	1.3	0.30	0.3590	-
2.50	48.18	-525.34	-0.03	80.9	2	76.9	77.6	3.1	0.12	0.3055	0.4448

Table 5. Summary of the results on the effect of fruiting seasonality on seed predation behavior.

Behavioral index	Predictions under predator satiation hypothesis	Effect	Applied analysis	Figure	Table
(1) Total feeding time	-	Positive	GLM	Fig. 2b	Table 1b
(2) Feeding time on seeds	-	Positive	GLM	Fig. 2a	Table 1a
(3) Number of species whose seeds are eaten	Positive	Positive	Correlation	Fig. 3a	
(4) Number of individuals whose seeds are eaten	Positive	Positive	Correlation	Fig. 3b	
(5) Average feeding time spent on seeds per species	Negative	None	GLM	Fig. 4a	Table 2a
(6) Average feeding time on seeds per individual plant	Negative	None	GLM	Fig. 4b	Table 2b
(7) Feeding time on seeds for the most frequently eaten species	Negative	Positive	GLM	Fig. 5a	Table 3a
(8) Feeding time on seeds for the most frequently eaten individual plants	Negative	Positive	GLM	Fig. 5b	Table 3b
(9) Duration of one seed-feeding event	Negative	None	GLM	Fig. 6	Table 4

order to avoid an overload of secondary compounds.

Do the red leaf monkeys change the degree to which they persist in pursuing one species/ individual of seeds in response to the changes in community-level fruit availability?

We found no support for this question. We showed that red leaf monkeys did not change their

average seed-predation time for each species or individual in response to the changes in fruit availability (Table 5). The duration of one seed-predation event was also unaffected by fruit availability in the same month. While seed-predation times for the most frequently eaten species or plant individuals tended to be long when fruit availability was high, the results for the most frequently eaten seeds were opposite to what would

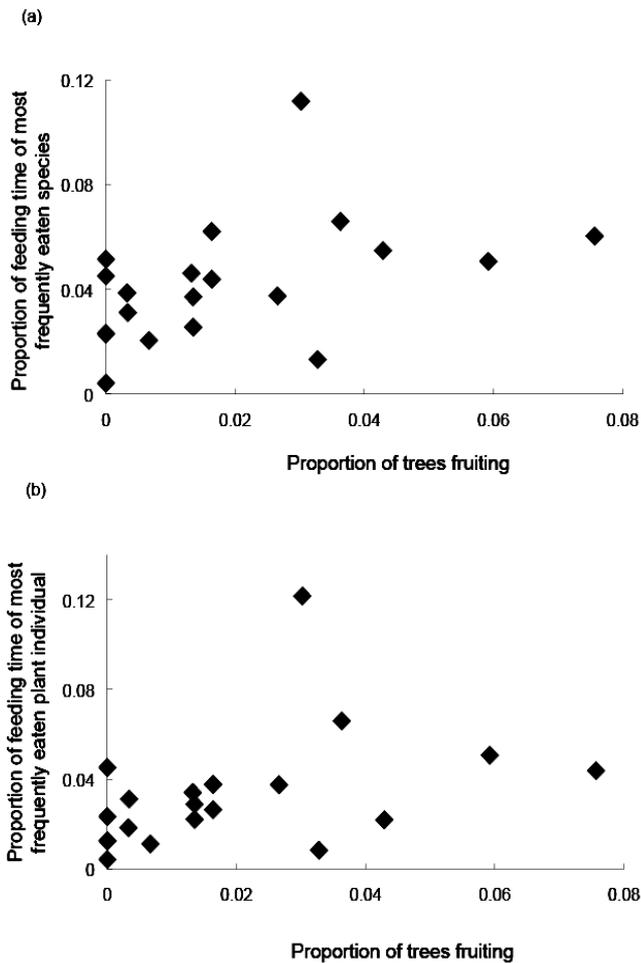


Fig. 5. The proportion of trees producing fruit eaten by red leaf monkeys in relation to the proportion of time spent feeding on most frequently eaten seed food (a) species seeds and (b) plant individuals.

be expected if monkeys tried to persist in eating one particular species/individual when overall fruit availability decreased. This must be a natural consequence of the larger number of species or individuals in the months of high fruit availability. Hence, contrary to the expectations of the predator satiation hypothesis, our findings show that red leaf monkeys do not persist on one species and/or increase their seed-feeding time per species or per individual plant. Although seeds seem to be preferred foods for red leaf monkeys, they do not increase their feeding effort on seeds when availability decreases.

In addition to the elongated feeding time of red leaf monkeys, several other explanations exist, for why our findings contradict the predator satiation hypothesis.

First, red leaf monkeys do not need to persist

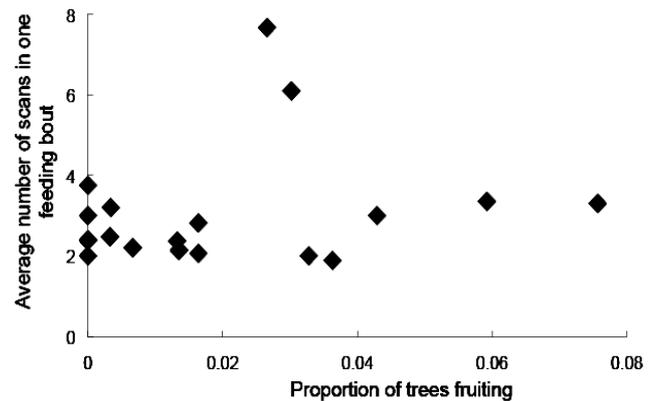


Fig. 6. The proportion of trees producing fruit eaten by red leaf monkeys in relation to the average duration of one seed-feeding event (unit: number of scans, conducted every 10 minutes) in that month.

in eating seeds because they can switch their diet to young leaves. Young leaves are a more abundant resource than fruits which translates to a lower searching cost. A similar effect of alternative resources in functional response is also observed in the North American red squirrel (Fletcher *et al.* 2010). Specifically, the proportion of spruce seeds depredated by the red squirrel varied with respect to the availability of alternative resources (mushrooms). When mushroom availability was low, the proportion of depredated seeds increased with decreasing spruce seed availability. When mushrooms were widely available, the proportion of depredated seeds was constant regardless of the changes in spruce seed availability.

Second, the degree of mast fruiting during our study period may not have been large enough to result in predator satiation. In Lambir Hills, Sarawak, more than 30 % of individual plants bore fruit at the peak of mast fruiting (Sakai 2002), which is markedly higher than the 6.7 % of individual plants that bore fruit at the peak of our study. Direct comparison is impossible because the procedure to select monitored trees was not specified in Lambir Hills. However, considering that no fruiting of dipterocarps was observed during our study period, an even larger fruiting peak is likely to occur on a longer time scale. If the fruit availability is extremely high, seed predation per species/individuals may decrease.

Third, the response by red leaf monkeys may have varied with respect to their preferences for each species of seed, since the eaten seeds include various taxonomic groups. When only less preferred seed species were available, monkeys did not spend

much time on seed predation. On the contrary, when only preferred seeds were available, monkeys depredated the seeds intensively and thus increased their total amount of seed predation. Studies on colobines, including the current study subjects, indicate that nutritional content, in particular protein content, affect colobine food selection, but secondary compounds do not (Chapman & Chapman 2002; Hanya & Bernard 2012; Kar-Gupta & Kumar 1994; Kool 1992; Yeager *et al.* 1997). Most of these studies are on leaf selection, but it is likely similar mechanism works for seed selection. Variable chemical contents may explain the variable degree of seed predation in periods when the fruit availability was intermediate or low.

Finally, the variable responses among months of low fruit availability might be due to the short observation time (40 h). This amount of observation time is not necessarily short compared to other studies on primate diet, and it is considered to be enough to describe general dietary characteristics (Hanya 2004a; Kaplin & Moermond 2000; Su & Lee 2001). Although the short observation time per month would make the results ambiguous, it is unlikely that it creates bias in any particular direction, since we have data for many months.

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