16 Seasonality of Fruiting and Food Hoarding by Rodents in Neotropical Forests: Consequences for Seed Dispersal and Seedling Recruitment

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Introduction

> Climatic variation causes a season of scarcity and the agoutis hoard seeds to overcome this.
> (Smythe, 1978, p. 48)

Fruit resource availability is highly seasonal in many tropical forests (Leigh, 1999; Wright *et al.*, 1999). Within-year variation in the diversity and abundance of food resources imposes dietary restrictions on animals by requiring them to consume what food is available in time and accessible in space. During periods of peak fruit abundance, many frugivores forage on the same species of fruiting trees (e.g. Guillotin *et al.*, 1994). When fruit is scarce, diets diverge as vertebrates with different body masses, home-range sizes and foraging tactics seek alternative resources in different ways. For example, peccaries (*Tayassu tajacu*) switch from fruit to worms, and spiny rats (*Proechimys cuvieri* and *Proechimys guianensis*) switch from fruit to insects (Henry, 1994a). The agouti (*Dasyprocta* spp.) and the acouchi (*Myoprocta* spp.), however, are exceptions. They remain frugivorous throughout the year, but alternate from pulp-centred to seed-centred diets during periods of high and low fruit production, respectively (Henry, 1999). In both South and Central American forests, these caviomorph rodents survive during lean periods by eating the seeds they buried when fruit was abundant (Smythe, 1970, 1978; Henry, 1999).

Seed hoarding is crucial to the survival and reproduction of many rodent species (Smythe, 1978; Henry, 1994b; Stapanian, 1986; Vander Wall, 1990). Seeds consumed during lean periods are assumed to be taken from caches or from seedlings with long-lasting seed reserves. In general, food caching takes place in anticipation of a decline in resource availability (e.g. winter in the temperate regions, the dry season in the tropics) by animals that cannot

Seed Dispersal and Frugivory: Ecology, Evolution and Conservation (eds D.J. Levey, W.R. Silva and M. Galetti)

meet their energetic requirements through body fat reserves alone. Seed removal and scatter-hoarding rates most probably depend on seasonal patterns of fruit availability, animal foraging and reproductive behaviour (Smythe, 1978; Dubost, 1988; Henry, 1994b). In temperate regions, it is well known that seed caching peaks when large-seeded plants fruit (Stapanian, 1986; Vander Wall, 1990). In these regions, rodent foraging behaviour may also depend on photoperiod or on interactions between external signals (e.g. day length, food availability) and internal states (e.g. hormone and hunger levels), both of which affect agonistic, reproductive and hoarding behaviour (Vander Wall, 1990; Henry, 1997).

Smythe (1978, p. 25) observed in Panama ‘that during times of food abundance, all agoutis hoard considerably more seeds than they eat’ and ‘when falling fruit becomes scarce, agoutis live almost entirely on scatterhoarded seeds’. Despite recurrent references to the seasonality of rodent seed caching in neotropical forests (Morris 1962; Rankin, 1978; Smythe, 1970, 1978; Vandermeer *et al.*, 1979; Hallwachs, 1986), we lack a theoretical framework for determining the effect of seasonal fruit availability on caching rates and, further, for investigating the implications of this seasonal dependence for plant and animal fitness.

How is seed-hoarding behaviour regulated or triggered in relation to seasonal fluctuations in food abundance in neotropical rain forests? How does seed caching affect pre- and post-dispersal insect seed predators? How does food scarcity affect the residence time of cached seeds? When food is abundant, does caching decline or stop, leaving many seeds vulnerable to other vertebrate and invertebrate seed predators (Smythe, 1970)? Such questions remain largely unexplored.

The aim of this chapter is to present a general, annually based model for hoarding in neotropical forests inhabited by large caviomorph rodents. We first summarize data on the range of seed removal and predation–hoarding ratios for four large-seeded tree species in one neotropical rain forest. Based in part on data collected for these four species, we then present a model of seed hoarding in relation to fruit resource abundance. Finally, we discuss the model’s implications for seed fate and seedling recruitment in light of the recent literature on seed dispersal by neotropical rodents.

Patterns of Seed Removal and Seed Fate: Data from Barro Colorado Island

The impact of rodents as seed predators and dispersers was analysed during a 1-year fruiting cycle in 1990 on Barro Colorado Island (BCI), Panama. On BCI, fruit is generally abundant during a 6-month period, from February to July, with peak fruit diversity roughly in the middle of this period (Smythe, 1970; Foster, 1982; Wright *et al.*, 1999). According to Smythe (1978), this is a period of intense seed caching. We expect that, as fruit abundance increases, animals probably become satiated and destroy a decreasing proportion of all seeds and fruits available. Before and after peak fruit fall, rodent removal and consumption of fallen fruits and seeds is proportionately greater. Based on preliminary observations of seasonal seed removal and hoarding in Panama, Costa Rica and French Guiana (Smythe, 1978; Hallwachs, 1986; Forget, 1990), we predict that the proportion of seeds hoarded will peak shortly after fruit production peaks in a community. To assess this prediction, we report seed-removal and seed-fate experiments carried out between January and October 1990, using *Dipteryx panamensis* (*Fabaceae*), *Astrocaryum standleyanum* (*Arecaceae*), *Gustavia superba* (*Lecythidaceae*) and *Attalea butyraceae* (*Arecaceae*). Seeds of each species have largest diameter > 1.5 cm and consist of single-seeded, nutlike fruits (*D. panamensis*, *A. standleyanum* and *A. butyraceae*) or of large, multiple-seeded capsules (*G. superba*) (Smythe, 1970). Because of minimal overlap in fruiting periods of these species over an annual cycle (D. Windsor, Terrestrial Environmental Sciences Program, personal communication), these four species are key resources for scatter-hoarding rodents, such as agoutis, squirrels and spiny rats; together they provide food throughout the year on BCI (Heaney and Thorington, 1978; Glanz *et al.*, 1982; Smythe *et al.*, 1982; De Steven and Putz, 1984; Sork, 1987; Smythe, 1989; Wright, 1990; Adler, 1995). For these tree species, we present 1 year of seed-fate data, upon which we then build a general model of seed hoarding.

Experiments with *D. panamensis* seeds were conducted in late January and replicated in late February and March 1990, using thread-marked seeds to locate and determine the fate of removed seeds (Forget, 1993). Most seeds were removed by agoutis (*Dasyprocta punctata*). Pooled data show that the per cent of seeds cached (from initial locations > 50 m from fruiting trees, simulating primary seed dispersal by bats) was lowest in February and April and highest in March (Fig. 16.1a), when seeds accumulated beneath parent trees and were eaten by rodents and peccaries (see De Steven and Putz, 1984). Caching of *D. panamensis* seeds therefore reached a maximum just after peak fruit fall of this species.

By April–May, fruit biomass and diversity are at their maximum on BCI. The abundant fruit appears to saturate rodents, leading to accumulation of uneaten seeds (Wright, 1990). Assuming that caching is triggered by food satiation (e.g. Vander Wall, 1990), we expect higher seed removal and caching rates by rodents at this time. Using a population of seven *A. standleyanum* palms, which occupied the intersection of several agouti home ranges, Milleron and Forget (1997) placed two groups of 25 thread-marked seeds under each of five palms, first on 30 April and then on 19 May 1990. We checked seed removal 12 h after the 6:00 a.m. seed placement, and searched for seeds within a 20 m radius of each palm. A large proportion of seeds (91%) were taken within 12 h; all were removed within a week. Most seeds in each trial were not found within 20 m. A smaller proportion was cached and eaten (Fig. 16.1b). We also observed mammal activity under individual palms in two continuous sessions of 3 h and 12.5 h from 9 to 13 June. During these observations, a majority of *A. standleyanum* seeds handled (*n* = 105) by *D. punctata* were cached (61%). The rest were eaten (19%) or removed at least 20 m (20%). If seeds removed > 20 m were cached, as direct observations of foraging animals suggest (Milleron and

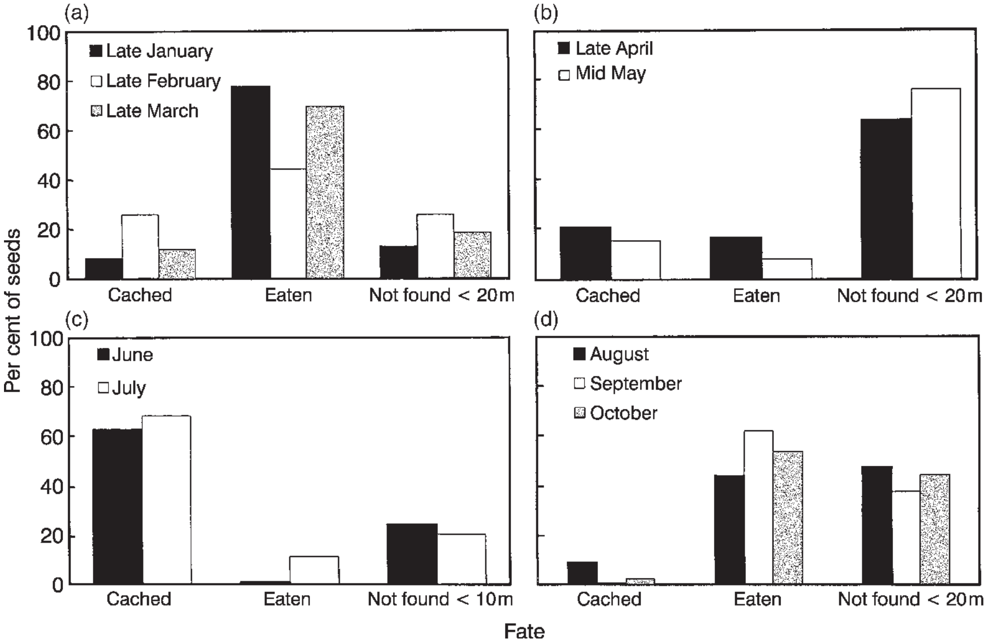

Fig. 16.1. Seed fate in (a) *Dipteryx panamensis* (out of *n* = 320 seeds per month), (b) *Astrocaryum standleyanum* (*n* = 250 seeds per month), (c) *Gustavia superba* (*n* = 200 seeds per month) and (d) *Attalea butyraceae* (*n* = 400 seeds per month) in 1990 at Barro Colorado Island, Panama. (Adapted from Forget, 1993; Forget *et al.*, 1994, 1998; Milleron and Forget, 1997).

Forget, 1997), then our results are consistent with Smythe's (1978) assertion that, when food is abundant, agoutis cache considerably more than they eat – in this case, approximately four seeds were cached for every seed eaten in May–June. Fates of the cached seeds were undetermined. They were rapidly removed, probably taken by rodents to secondary caches (see Jansen and Forget, 2001). Indeed, we occasionally retrieved cached seeds > 100 m from their origin. These seeds had been marked as cached within 20 m of their origin (T. Milleron and P.-M. Forget, personal observations).

Experiments with *G. superba* showed that seed removal was significantly higher in July (100%), when fruit was less abundant, than in June (88%), when fruit was more abundant. Unremoved seeds germinated but all were later eaten by vertebrates. The majority of seeds retrieved within 10 m of their deposition site were cached and few seeds were eaten; the remainder were assumed to be cached further away (Forget, 1992; Forget *et al.*, 1998) (Fig. 16.1c). (Of cached seeds, approximately 13% established and survived in the short term, despite high post-dispersal predation upon germination, especially by rodents (Forget *et al.*, 1998; Dalling and Harms, 1999).)

As food diversity declines on BCI, the spatial distribution of resources becomes concentrated around the few scattered tree species that drop their fruit in July–August (e.g. *A. butyraceae* (Wright, 1990)). All seeds placed beneath four fruiting *Attalea* palms during this period were removed. The majority were eaten and a few were cached < 20 m away (Fig. 16.1d). As in *A. standleyanum*, all of the dispersed seeds were removed by rodents in the following weeks, to be either consumed or recached.

A Model for Seed Fate: Hoarding versus Predation

> When an agouti encounters a concentrated food source, it usually eats a few of the fruits or seeds and then starts to bury them.
>
> (Smythe, 1978, p. 25)

Tropical rodents rely principally on caches – rather than stored body fat – to survive lean periods and, because the daily amount of food they consume is relatively constant throughout the year (e.g. Henry, 1999), seed-caching behaviour probably mirrors the seasonality of fruit and seed resources. On BCI, a 1-year fruiting cycle can be roughly divided in half: a 6-month period of relatively abundant fruit in February–July and a 6-month lean period in June–January (Wright *et al.*, 1999) (Fig. 16.2a). Using the large data set from BCI (1987–1999) and performing a Fourier analysis in the time-series procedure of Systat 9 (SPSS, 1999) on the number of species bearing fruit between January 1987 and December 1999 (O. Calderon and S.J. Wright, personal communication), we fitted data from three sets of four consecutive years (1987–1990, 1991–1994 and 1995–1998) to a sine-wave function. Using the entire 12-year data set, only a 1-year (annual) cycle was evident (data not shown), strongly demonstrating the seasonal periodicity of fruiting on BCI. We expect the hoarding behaviour of rodents to be more tightly related to three 4-month periods (high, declining and low) than to two 6-month periods (peak versus lean) of fruiting. Accordingly, we followed Guillotin *et al.* (1994) and delimited three 4-month periods of fruit diversity summing to the annual cycle for BCI (Table 16.1). Periods were defined as follows: (i) a high fruit season (HFS), centred on the 2 months with the highest fruit diversity; (ii) a declining fruit season (DFS) period, corresponding to a decrease in fruit diversity; and (iii) a low fruit season (LFS), characterized by an increase in fruit diversity, starting from the annual low of fruit diversity.

Data on the percentage of seeds (out of the number of seeds placed) known to be cached and the percentage assumed to be cached (i.e. not found at < 10 or 20 m) were pooled. These 'hoarded seeds' are not necessarily scatter-hoarded seeds, but include those taken to other types of caches in burrows or trees; this is equivalent to seed burial from the animal's perspective. Seed removal is therefore considered equivalent to hoarding, as is often reported in seed-predation studies. However, our use of seed-removal data excludes de facto the fraction of fallen seeds that are immediately consumed by invertebrates and vertebrates, defined *sensu stricto* as pre- and

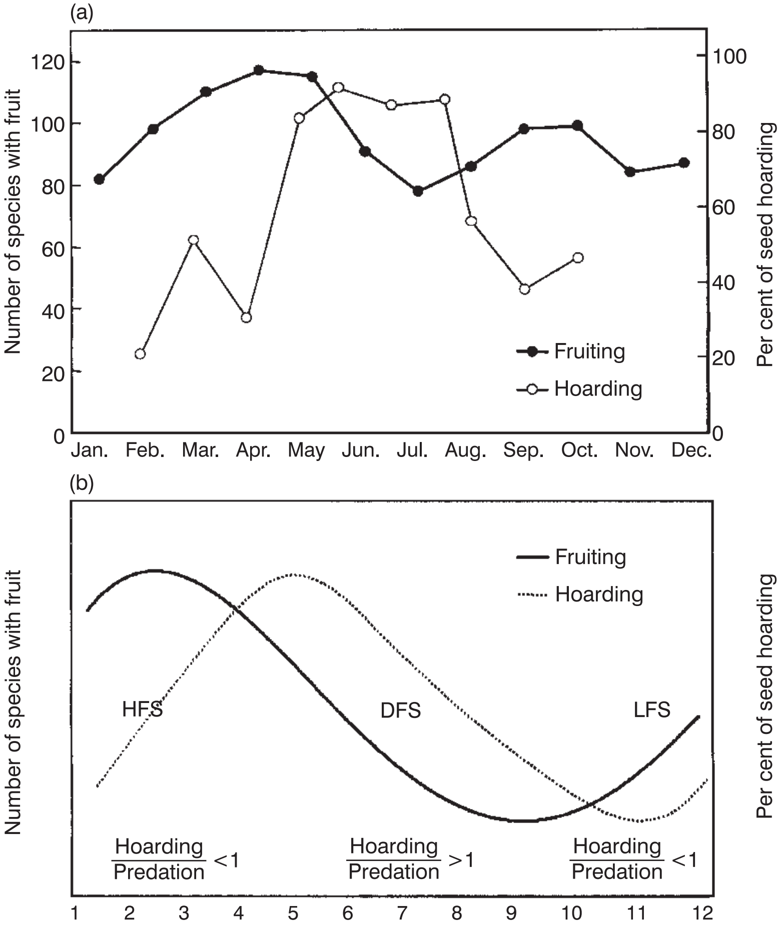

Fig. 16.2. (a) Seasonal fruit-fall pattern and level of hoarding activity for the four study species in the study year (1990) (O. Calderon and S.J. Wright, personal communication). (b) Model of fruit-fall pattern and intensity of hoarding activity during a 1-year cycle, and expected ratio of % seed hoarding vs. % seed predation in the three fruiting seasons. HFS, high fruit season; DFS, declining fruit season; LFS, low fruit season. See text for explanation. The fruiting curve is the polynomial function ($y = -0.0051x^5 + 0.1186x^4 - 0.2607x^3 - 8.1973x^2 + 35.444x + 87.788$; $R^2 = 0.96$), which best fits the data at Paracou, and the hoarding curve was drawn based on results from BCI (Fig. 16.1 and 16.2a) and Paracou (Forget, 1996).

post-dispersal seed predation. The data reveal a temporal pattern, with the maximum proportion of hoards made in the transition between HFS and DFS (Fig. 16.2a).

A graphical model of seed hoarding (as defined above) (Fig. 16.2b) follows the pattern of fruiting with a time-lag of approximately 2 months. First, when the number of fruiting species and fruit biomass is peaking (HFS), seed hoarding should be low, with a hoarding/predation ratio < 1, because rodents are satiated. When the diversity of fruit is highest, resources are widely distributed and rodents probably have access to fruit over their entire home range. Due to both low caching and low predation by rodents, a large fraction of seeds may lie where they fall. Hoarding increases toward the end of the fruit peak, when fruit diversity starts to decline.

Secondly, when fruit diversity is declining (DFS), fruit resources are often concentrated beneath a few, often large-seeded species. Although rodents at this time are not yet food-limited, the difference in spatial distribution of

Table 16.1. Mean number (± SD) of fruiting species during three fruiting seasons and corresponding months in five neotropical rain forests.

					Fruiting season		
Field station	Country	Period	Method	Location	HFS	DFS	LFS
BCI[*]	Panama	1987–1999 (13 years)	Fruit traps	9° 9′ N, 79° 51′ W	82.8 ± 12.9 (Mar.–Jun.)	56.7 ± 2.0 (Jul.–Oct.)	51.1 ± 9.3 (Nov.–Feb.)
Mabura Hill[†]	Guyana	1997–1998 (2 years)	Fruit traps	5° 13′ N, 58° 48′ W	12.8 ± 3.1 (Feb.–May)	5.8 ± 0.5 (Jun.–Sep.)	7.8 ± 1.2 (Oct.–Jan.)
Paracou[‡]	French Guiana	1989–1991 (2 years)	Raked trail censuses	5° 16′ N, 52° 55′ W	29.0 ± 4.0 (Jan.–Apr.)	14.5 ± 6.7 (May–Aug.)	11.8 ± 4.9 (Sep.–Dec.)
Pinkaití[§]	Brazil	1996–1998 (2 years)	Tree censuses	7° 46′ S, 51° 57′ W	24.9 ± 2.9 (Aug.–Nov.)	18.4 ± 4.8 (Dec.–Mar.)	15.9 ± 5.6 (Apr.–Jul.)
Cocha Cashu[‖]	Peru	1976–1977 (12 months)	Fruit traps	11° 54′ S, 71° 22′ W	12 ± 1.2 (Sep.–Dec.)	6.5 ± 5 (Jan.–Apr.)	3.8 ± 2.2 (May–Aug.)

[*] Wright *et al*. (1999) and O. Calderon and S.J. Wright (personal communication).

[†] Thomas (2000).

[‡] Henry (1994a) and O. Henry (personal communication).

[§] Baider (2000).

[‖] Terborgh (1983) and J. Terborgh (personal communication).

HFS, high fruit season; DFS, declining fruit season; LFS, low fruit season.

resources over their home range may trigger them to hoard seeds before the season of scarcity, just as temperate rodents do in the autumn for consumption in the winter (Stapanian, 1986; Vander Wall, 1990). During this second period, seed-caching rates will steadily increase and predation will remain low, leading to a hoarding/predation ratio > 1. The greater the rodents' reliance on their hoards, the less they will cache seeds they encounter during foraging and the greater their predation on any seeds encountered.

Finally, during a period of low fruit diversity (LFS), predation will probably surpass hoarding, with, for example, two to five seeds cached versus eight seeds eaten (ratio hoarding/predation < 1), as observed in *D. panamensis* in February, when community-wide fruit production was on the upswing (Forget, 1993) (Fig. 16.1a). Evidence of a similar hoarding/predation ratio was observed during the mid-LFS for a large-seeded liana, *Gnetum loyboldii* (*Gnetaceae*), which fruits in August–November on BCI (P.M. Forget, personal observation). Despite heavy predation on freshly fallen seeds, some seeds were obviously cached, as remains of *G. loyboldii* seeds were retrieved that had been dug up and gnawed as late as late February. As fruit diversity increases, rodents progressively hoard seeds in greater proportion to those they consume. Among small-seeded species, however, fruiting when fruit diversity is increasing may lead to significant seed predation and low, if not nil, secondary seed dispersal (Hammond, 1995; Forget *et al.*, 1998).

Supporting Evidence from Other Neotropical Sites

Approximately 20 years after Vandermeer *et al.* (1979) emphasized the lack of information on seed fate, an increasing number of studies are documenting seed fate across the neotropics (Table 16.2). Here we assess seed fates in relation to fruit-fall seasonality to evaluate our model. The methodology used to document fruiting seasonality is inconsistent among sites. The number of species in fruit per month is sometimes based on traps (Cocha Cashu: Terborgh, 1983; Mabura Hill: Thomas, 2000), on ground samples along transects (Paracou: Henry, 1994a) or on direct counts of mature fruit in tree crowns (Pinkaití: Baider, 2000) (Table 16.1). We assume that seasonal oscillation in fruit production is well defined and that the accuracy of each method in detecting seasonal peaks and troughs is similar. Several studies quantify both the mean number of species and the overall mass of fruit produced, showing a clear correlation between the diversity and abundance of fruit (Smythe, 1970; Sabatier, 1985; Terborgh, 1986; Wright *et al.*, 1999). We use the average number of species in fruit per month because it is the metric common to all studies. For Cocha Cashu and Paracou, censuses were biweekly but we used only the mid-month censuses.

The high fruiting season (HFS)

In French Guiana, agoutis (*Dasyprocta leporina*) rely mostly on pulp (48% of diet in fruit-item dry mass) (data in Henry, 1999), not on seeds (21%) in HFS. As a consequence, their impact as seed predators as well as secondary seed-dispersers should be minimal during this season. This is supported in Mabura Hill, Guyana, where 43% of unprotected *Chlorocardium rodiei* (*Lauraceae*) seeds monitored in HFS had been handled by vertebrates. Most (74%) were removed (some probably cached) and only 3% were eaten; the remainder were infested by bruchids (80%) or attacked by ants (10%) (Hammond *et al.*, 1999). In Paracou, French Guiana, *Virola michelii* seeds are rarely taken and secondarily dispersed by rodents in HFS (Forget *et al.*, 2000). Similarly, 77% of marked *Carapa procera* seeds remained after 4 weeks in HFS in Paracou, approximately one seed being hoarded for each seed eaten by rodents (assuming unrecovered seeds were cached further than 10 m) (Forget, 1996). In Paracou, during the HFS, all *Astrocaryum paramaca* seeds were removed by spiny rats and acouchies (*Myoprocta exilis*): 68% were cached, 7% were eaten beneath fruiting palms and the remainder had unknown fates (Forget, 1991).

In Pinkaití, Brazil, Peres and Baider (1997) observed that agoutis (*D. leporina*) rapidly removed and dispersed *Bertholletia excelsa*

Table 16.2. Field studies on post-dispersal seed removal by vertebrates (mostly rodents), observed and expected seed fates in neotropical rain forests during three fruiting periods.

Country	Site	Study species	Study period	Fruit period	Removal (%)	Observed fate	Expected fate	Author
Mexico	Chiapas	*Bursera simaruba*	May	HFS	94	P > H		Hammond (1995)
		Erythrina goldmanii	May		25	H = P		
		Swietenia humilis	May		37	P > H		
		Spondias mombin	July	DFS	76	H > P		
Belize	Bladen Nature Reserve	*Astrocaryum mexicanum*	February–March	HFS	73	P > H		Brewer and Rejmanek (1999)
		Ampelocera hottlei	May	HFS	96	P > H		
		Pouteria sapota	May	HFS	34 (site A)	P > H		
			July–September	DFS	62 (site B)	H ≈ P		
	Bladen Nature Reserve	*Astrocaryum mexicanum*	September–October	LFS	90–100	P > H		Brewer (2001)
Costa Rica	Santa Rosa	*Hymenaea courbaril*	January	LFS	95 (pod)	No data	P > H	Hallwachs (1986)
			March	HFS	12 (pod)	No data	P = H	
			August	DFS	100 (pod)	No data	H > P	
	La Selva	*Welfia regia*	March	HFS	100	P > H		Guariguata *et al.* (2000)
		Minquartia guianensis	April	HFS	100	P > H		
		Virola koschnyi	April	HFS	100	P > H		
		Otoba novogranatensis	April	HFS	97	P > H		
		Lecythis ampla	May	HFS	100	P > H		
		Carapa nicaraguensis	July	DFS	100	P > H		
	La Selva	*Carapa nicaraguensis*	July–September	DFS	54–96	No data	H > P	MacHargue and Harsthorn (1981)
	La Selva	*Welfia regia*	July	DFS	80	No data	H > P	Schupp and Frost (1989)

	La Selva	*Welfia regia*	July–August	DFS	9	No data	H > P	Vandermeer *et al*. (1979)
			September	DFS	15			
			October		49			
	Monteverde	*Ocotea endresiana*	May	HFS	100	P > H		Wenny (2000)
	Monteverde	*Guarea glabra*	June–August	HFS–DFS	95	H > P		Wenny (1999)
		Guarea kunthiana	June–August		100	H > P		
Panama	BCI	*Faramea occidentalis*	January–July	LFS–HFS	*c*. 10–70	No data	P > H H = P	Schupp (1990)
	BCI – Gigante	*Dipteryx panamensis*	January–February	LFS	73–100	No data	P > H	De Steven and Putz (1984)
	BCI	*Dipteryx panamensis*	February–April	LFS–HFS	96–100	P > H		Forget (1993)
	BCI – Gigante – Gatun Lake	*Dipteryx panamensis*	March	HFS	99–100	No data	P > H	Asquith *et al*. (1997)
	BCI	*Astrocaryum standleyanum*	April–May	HFS	100	H > P		Milleron and Forget (1997)
	BCI	*Virola nobilis*	June	HFS	52	H > P		Forget *et al*. (1998)
		Brosimum alicastrum	June		86	P > H		
	Gatun Lake	*Attalea butyraceae*	June	HFS	16	H > P		Adler and Kestell (1998)
	Gatun Lake	*Callophyllum longifolium*	June	HFS	54	P > H		
	BCI	*Gustavia superba*	June–July	HFS–DFS	88–100	H > P		Forget *et al*. (1998)
	BCI	*Gustavia superba*	July	HFS	98	P > H		Asquith *et al*. (1997)
	Gigante				100	H > P		
	Gatun Lake				84–100	P > H		
	BCI	*Licania platypus*	July–August	DFS	99–100	P > H		Forget *et al*. (1998)
	BCI	*Attalea butyracea*	July–September	DFS	100	P > H		Forget *et al*. (1994)
	BCI	*Virola nobilis*	August	DFS	100	P > H		Asquith *et al*. (1997)
	Gigante				100	H > P		
	Gatun Lake				100	P > H		
	BCI	*Cupania latifolia*	August	DFS	100	P > H		Forget *et al*. (1998)
		Doliocarpus olivaceus	August		91	P > H		
		Eugenia coloradensis	August		96	P > H		

continued

Table 16.2. *Continued.*

Country	Site	Study species	Study period	Fruit period	Removal (%)	Observed fate	Expected fate	Author
Trinidad		*Carapa guianensis*	November–February	LFS	60–100	No data	P > H	Rankin (1978)
Guyana	Mabura Hill	*Chlorocardium rodiei*	February–March	HFS	32	H > P		Hammond *et al.* (1999)
French Guiana	Paracou	*Virola michelii*	January	HFS	64	P > H		Forget *et al.* (2000)
	Paracou	*Carapa procera*	March	HFS	23	P > H		Forget (1996)
			April–May	HFS–DFS	75–96	H > P		
	Nouragues	*Vouacapoua americana*	May	DFS	94–100	H > P		Forget (1990)
	Paracou	*Astrocaryum paramaca*	March	HFS	100	H > P		Forget (1991)
Brazil	Pinkaïti	*Bertholletia exelsa*	February	DFS	90	No data	H > P	Peres *et al.* (1997)
			October	HFS	82.5		H = P	
	Pinkaïti	*Bertholletia exelsa*	October	HFS	88	H > P		Peres and Baider (1997)
Peru	Cocha Cashu	*Astrocaryum macrocalyx*	October	HFS	91–97	No data	H = P	Terborgh *et al.* (1993)
		Dipteryx micrantha	October		97			
		Hymenaea courbaril	October		69–81			
		Bertholletia exelsa	October		100			
	Cocha Cashu	*Dipteryx micrantha*	June	LFS	98	P > H		Cintra (1997)
	Jenaro Herrera	*Macoubea guianensis*	July	LFS	95	No data	P > H	Notman *et al.* (1996)
		Pouteria sp.	July		25			

H, hoarding; P, predation; HFS, high fruit season; DFS, declining fruit season; LFS, low fruit season.

(*Lecythidaceae*) seeds in the late HFS. Of 709 marked seeds, 14% were found intact, 44% buried, 2% eaten and 40% not found in October–November (after Table 1 in Peres and Baider (1997)). Peres and Baider (1997) observed a hoarding/predation ratio > 1 for *B. excelsa* with up to seven seeds cached per seed eaten. This result is similar to that of *C. procera* in French Guiana with roughly three seeds cached per seed eaten in late HFS (Forget, 1996).

The declining fruiting season (DFS)

Agouti diets change during the DFS in French Guiana (Henry, 1999), becoming more focused on seeds than pulp. Overall, seeds and pulp accounted for 44.6% and 24.6% of fruit items in DFS, respectively, in reverse proportion to HFS values (after Henry, 1999). In both Guyana and French Guiana, many large-seeded species, including *Astrocaryum sciophilum*, *Attalea maripa* (*Areacaceae*), *Dipteryx punctata* (*Fabaceae*), *Licania alba* (*Chrysobalanaceae*), *Carapa procera* (*Meliaceae*), *Moronobea coccinea* (*Clusiaceae*), *Platonia insignis* (*Clusiaceae*), *Andira inermis* (*Fabaceae*), *Vouacapoua americana* and *Vouacapoua macropetala* (*Caesalpiniaceae*) fruit in the DFS (Sabatier, 1985; Sist, 1989; Forget, 1990, 1991, 1996; Ter Steege and Persaud, 1991; Jansen and Forget, 2001; P.-M. Forget, personal observation), and are clearly rodent-dispersed species (Hammond *et al.*, 1996; Forget and Hammond, 2001; D.S. Hammond, personal observation). In Paracou, seed removal in *C. procera* increases during the DFS, representing seed dispersal by rodents with an average of ten seeds hoarded for each one eaten (Forget, 1996).

The low fruit season (LFS)

Rodent reliance on seeds probably reaches a maximum during the LFS, when few fruit and seed resources are available above ground. In a pilot experiment carried out in LFS at Cocha Cashu, Peru, Cintra (1997) studied the fate of magnet-labelled seeds of *Dipteryx micrantha* and *Astrocaryum murumuru* and found that most removed seeds were preyed upon by rodents. Additional studies are needed in which seeds are stored during peak periods of community-level fruit production for use in seed-fate studies during the LFS.

Variation in seed fate among sites

While studying the effect of local faunal extinction and mammalian exclusion, Guariguata *et al.* (2000) showed that removal rates of medium-sized (2–4 g) and large (6–20 g) seed species were high in HFS at La Selva, which has a fruiting pattern comparable to that of BCI (M. Guariguata, personal communication; see also Loiselle *et al.*, 1996). However, Guariguata *et al.* (2000) observed that only a small proportion (*c.* 8%) of medium-sized seeds was scatter-hoarded within 10 m, suggesting that they were taken mostly by spiny rats (*Heteromys desmarestianus*). A similar result was obtained by Brewer and Rejmanek (1999) by Brewer (2001), and by Brewer and Webb (2001) in Belize, where high removal of *Astrocaryum mexicanum*, *Ampelocera hottlei* (*Ulmaceae*) and *Pouteria zapota* (*Sapotaceae*) in HFS (March–June) and the rest of the year (S. Brewer, personal communication) is explained by seed predation by *H. desmarestianus*. In Monteverde, Costa Rica, Wenny (1999, 2000) showed that seed size influenced whether seeds were eaten or scatter-hoarded, despite overall high seed-removal rates in HFS and DFS. Adler and Kestell (1998) studied *Callophyllum longifolium* (*Clusiaceae*) and *A. butyraceae* seeds during the HFS in Panama on small islands with only one seed predator, spiny rats (*Proechimys semispinosus*), and found low seed removal and contrasting seed fates between species on islands lacking agoutis, the main seed disperser of such large seeds on BCI. Without agoutis, removal of *A. butyraceae* was low (16%) and a majority of seeds found had been cached by spiny rats. In contrast, removal of *C. longifolium* seeds was greater but mainly explained by predation. Seed-removal and hoarding rates in different fruiting seasons probably depend on the relative densities of small and large rodents (Adler, 1998). For example, Asquith *et al.* (1997) observed that 100% removal of *Virola nobilis* and *G. superba* seeds in DFS results in different seed fates between BCI, the mainland and islands in the Panama Canal Zone. Our model implicitly assumes that large rodents, such as agoutis and acouchies, whose scatter-hoarding behaviour contrasts with that of other seed-eaters, are present in sufficient numbers to compete for seeds with smaller rodents, peccaries and other vertebrates.

Implications for Plant Recruitment

In neotropical rain forests, the role of rodents as seed-dispersers or seed predators will probably fluctuate, depending on fruit morphology, seed size and fruiting phenologies. Whether rodents prey upon or disperse seeds has strong implications for seed survival and seedling recruitment. For example, on BCI the peak diversity in wind-dispersed diaspores of lianas and canopy-tree species (which comprise 25% of all woody species) occurs in March–May, the dry season (Foster, 1982) or the HFS (Table 16.1). In contrast, there are two peaks in fruit diversity among animal-dispersed tree species, one in May–June (late HFS) and another in September–October (LFS). In French Guiana, wind-dispersed species (6.8% of the woody species) fruit in the wet season at the same time as animal-dispersed species (Sabatier, 1985). A major consequence of such contrasting fruiting patterns between French Guiana and Panama may be that, when food is scarce during the dry season, large rodents will depend on different food sources at the two sites. Rodents in Panama will rely more upon wind-dispersed and large-seeded animal-dispersed species (Smythe, 1970, 1978; Smythe *et al.*, 1982; Forget, 1993; Forget *et al.*, 1999), while rodents in French Guiana will depend on cached seeds and cotyledons from germinating seedlings (Forget, 1996; Jansen and Forget, 2001). Seedling recruitment in all species, regardless of seed size or dispersal mode, during such periods of low food availability may thus depend on the capacity of local seed predators to become satiated (Janzen, 1971). This capacity will be determined by key resources, such as *Dipteryx* spp. seeds in both Central America and Peru (De Steven and Putz, 1984; Terborgh, 1986; Forget, 1993; Terborgh and Wright, 1994) or large seed crops, such as those of palms, which contribute greatly to hoards (e.g. Forget, 1992; Henry, 1999).

Smythe (1970, p. 33) proposed that 'seeds that are too large to be swallowed and are dispersed by hoarding rodents benefit from fruiting as nearly synchronously as possible'. This argument was based on the observation that large-seeded species, such as *A. standleyanum* or *G. superba*, fruit in May–June, the late HFS. In neotropical forests, large seeds dispersed by hoarding rodents often fruit during the same period, in the late fruiting season when rainfall is high, as in Guyana and French Guiana (Sabatier, 1985; Ter Steege and Persaud, 1991; Forget, 1996; Hammond *et al.*, 1999). Based on several studies of seed removal and fate, this period seems to be strongly characterized by agouti and acouchi caching behaviour (Table 16.3).

Studies on *C. procera* in French Guiana have shown that seeds not removed by rodents in February or March are destroyed by either peccaries or moths. The same patterns hold for several other seed species: *V. americana* seeds dry out or are killed by bruchids (Forget, 1990); *Attalea* spp. and *Astrocaryum* spp. seeds are killed by bruchids or peccaries (Janzen, 1971; Wright, 1983, 1990; Sist, 1989; Smythe, 1989; Terborgh *et al.*, 1993; Forget *et al.*, 1994; Silvius, 1999; Harms and Dalling, 2000); *B. excelsa* seeds rot due to fungal pathogens (Terborgh *et al.*, 1993, Peres and Baider, 1997); *Hymenaea courbaril* seeds are infested by weevils or crushed by peccaries (Janzen, 1983; Hallwachs, 1986); *Guarea kunthiana* seeds are eaten by peccaries and are insect-infested post-dispersal (Wenny, 1999). *Gustavia superba* may be an exception, as unremoved seeds are free from post-dispersal parasitism and germinate and survive on BCI when seed removal is low during a good crop year (Sork, 1987). However, this could be an artefact due to the low populations of large terrestrial vertebrates, especially peccaries, on BCI as observed for large accumulations of *C. procera* seeds at Paracou. There, peccary densities are very low due to hunting. Fruiting of large-seeded species may thus predominate as overall fruit diversity decreases, and caching by rodents is most likely.

Table 16.3 General climate of the three fruiting seasons and predictions drawn from the model on animal energetic state, diet diversity, the ratio between the percentage of seeds hoarded (H) by rodents and suffering predation (P) by all vertebrates and invertebrates, and the rodent seed-dispersal phase that dominates during each fruiting season.

	Fruiting season		
	HFS	DFS	LFS
Rainfall regime	Early to mid wet season	Late wet season	Dry season
Animal energetic state	Satiated	Triggered to hoard	Depleted
Diet diversity	High	Medium	Low
Ratio H/P	< 1 % H < % P	> 1 % H > % P	< 1 % H < % P
Dispersal phase	Secondary	Primary	Secondary

Studies carried out on islands where environmental factors have been modified by forest fragmentation reveal the range of responses to seeds in habitats lacking large rodents, peccaries and other large mammals (Leigh *et al.*, 1993; Asquith *et al.*, 1997; Adler and Kestell, 1998). When not protected from vertebrates and not cached, seeds are eaten by spiny rats on the mainland and BCI, but seeds survive for at least 1 year on the ground surface on small islands without granivores or at other sites when totally protected from vertebrates.

Large seeds (> 10 g) are less often dispersed by rodents during peak fruiting than subsequently, but this pattern may not hold for smaller seeds (< 5 g). This is because rodents are often secondary dispersers of small- to medium-sized seeds (e.g. Forget and Milleron, 1991; Forget, 1993; Asquith *et al.*, 1997; Forget *et al.*, 1998; Wenny, 1999, 2000; Guariguata *et al.*, 2000). The rate of secondary seed dispersal is highly variable within and between forests. Rodent population density and food availability may interact to create areas of low or high secondary seed dispersal or predation (Notman *et al.*, 1996; Forget *et al.*, 2000, 2001).

The proportion of small- to medium-sized seeds secondarily dispersed by rodents probably depends on the relative rewards of eating versus caching them. Seed species of medium size with a long period of dormancy will be good candidates for caching and, later, establishment. In contrast, edible seeds that germinate rapidly are more likely to be eaten immediately.

In summary, we propose that caviomorph rodent caching behaviour is regulated by a subtle ratio between fruit diversity (greater diversity indicating a broader spatial distribution of fruits) and abundance during the peak fruiting period; caching is greatest at the HFS–DFS transition. The satiation capacity of caviomorph rodents probably depends on the spatiotemporal availability of fruit resources over the rodent's home range and may determine areas favourable (or unfavourable) to primary or secondary seed dispersal or predation.

Acknowledgements

We are very grateful to the editors for their invitation to the symposium and workshop. We thank Doug Levey and the students in his Frugivory and Seed Dispersal course, Patrick Jansen, Tad Theimer and Steve Vander Wall for their constructive comments and suggestions for improving the clarity and presentation of the manuscript. P.-M. Forget would particularly like to thank Martine Perret and Fabienne Aujard (CNRS, Centre National de la Recherche Scientifique, Brunoy) for their help with the time-series statistics. Claudia Baider, Steven Brewer, Manuel Guariguata, Olivier Henry, Evan Notman, Kirsten Silvius, John Terborgh and Joe Wright contributed fruitful discussions during the preparation of this chapter. Thanks also to Joe Wright and Steve Paton for sharing the long-term fruit data set from BCI.

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