

## SCATTERHOARDING OF *ASTROCARYUM PARAMACA* BY *PROECHIMYS* IN FRENCH GUIANA : COMPARISON WITH *MYOPROCTA EXILIS*

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**Abstract:** The fate of seeds removed from *Astrocaryum paramaca* palms was examined both by night and day during the peak fruiting season of a palm community. Nocturnal seed-removal was principally due to *Proechimys* spp. (*P. cuvieri* and *P. guyannensis*), whereas *Myoprocta exilis* was responsible for most of the disappearance by day. Seed-dispersal experiments with a thread-marking method showed that *Proechimys* spp. scatterhoarded seeds for later consumption. Unlike *M. exilis*, spiny rats did not bury seeds in the ground but cached them under the litter. This contrasts with previous literature on the hoarding behavior of this rodent. Rodent seed removal rates were greater by night than by day. Despite high predation of nocturnal caches within six months after dispersal, some seeds survived and germinated following caching. *Proechimys* spp. were thus a reliable disperser of *A. paramaca*.

**Résumé :** Les rythmes diurnes et nocturnes de disparition, et le sort des graines d'*Astrocaryum paramaca* ont été étudiés pendant le pic de fructification d'une population de palmiers. La disparition des graines pendant la nuit est principalement due à *Proechimys* spp. (*P. cuvieri* et *P. guyannensis*), alors que de jour, *Myoprocta exilis* en est le principal responsable. Des expériences réalisées à l'aide de graines marquées par un fil, montrent que *Proechimys* spp. cachent les graines isolément, et les consomment ultérieurement. Le comportement de mise en réserve chez ce rongeur contraste avec la précédente littérature. Contrairement à *M. exilis*, les rongeurs épineux n'enfouissent pas les graines dans le sol mais les cachent sous la litière. Le taux de disparition des graines est plus élevé de nuit que de jour. En dépit d'une forte prédation moins de six mois après la dissémination, quelques graines survivent et germent dans les caches. Par conséquent, *Proechimys* spp. est un efficient disséminateur d'*A. paramaca*.

**Resumen :** El destino de las semillas removidas de las palma *Astrocaryum paramaca* fue estudiado tanto en la noche como en el día durante el período de fructificación de una comunidad de palmas. Durante la noche, la remoción de semillas es dada principalmente por *Proechimys* spp. (*P. cuvieri* y *P. guyannensis*), mientras *Myoprocta exilis* es responsable de la mayoría de las desapariciones de semillas durante el día. Experimentos de dispersión de semillas, usando el método de marcaje con hebras de hilo, mostraron que *Proechimys* spp. dispersaron las semillas separadas para consumo posterior. A diferencia de *M. exilis*, las ratas espinosas nunca enterraron semillas en el suelo pero las depositaron en escondrijos en la hojarasca. Esto contrasta con los reportes anteriores del comportamiento de estos roedores. La tasa de remoción de semillas por roedores fue mayor durante la noche que durante el día. Aunque hay una fuerte predación sobre las semillas 6 meses después de su dispersión, algunas logran sobrevivir y germinar luego. *Proechimys* spp. es así un agente dispersor eficiente de *A. paramaca*.

**Resumo :** Os ritmos diurnos e noturnos de remoção de sementes de *Astrocaryum paramaca* foram estudados o período de fructificação em comunidade de palmeiras. A remoção de sementes durante a noite se dá principalmente por *Proechimys* spp. (*P. cuvieri* e *P. guyannensis*) enquanto que durante o dia *Myoprocta exilis* é o principal responsável. Experimentos realizados utilizando-se sementes marcadas com fios, mostraram que *Proechimys* spp. dispersam as sementes isoladamente para consumo posterior. Diferentemente de *M. exilis*, ratos espinhosos nunca enterram sementes senão que as escondem no foliço. Este fato contrasta com o que diz a literatura sobre o comportamento destes roedores. A taxa de remoção de sementes foi muito mais elevada durante a noite que durante o dia. Apesar de intensa predação sobre as sementes durante os 6 meses após sua dispersão,

algumas logran escapar e germinar. *Proechimys* spp. é portanto um eficiente dispersor de *A. paramaca*.

**Key Words :** *Astrocaryum paramaca*, French Guiana, *Myoprocta exilis*, *Proechimys*, Scatterhoarding.

## INTRODUCTION

Studies on seed ecology of palm communities often focus on consumption by various animals, and the fates of dispersed seeds are not always described (Uhl & Dransfield 1987). Among the described relationships between rodents and palms in neotropical forests, there are many casual observations of seed predation but few of seed-dispersal.

Seed-removal is commonly associated with seed predation under the parent tree by terrestrial frugivorous mammals (cf. Smythe 1986). Rodents are major seed predators. Nevertheless, some neotropical caviomorph rodents such as acouchy (*Myoprocta* spp.) and agouti (*Dasyprocta* spp.) scatterhoard food (Morris 1962) in the field when fruits are abundant, and thereafter disperse seeds (Dubost 1988; Forget 1990a, 1990b; Smith & Reichman 1984; Smythe 1970, 1978, 1989; see also Price & Jenkins 1986; Vander Wall 1990). Although rodents act as post-dispersal predators on cached seeds (cf. Janzen 1970, 1971) and germinated seeds through the period of fruit scarcity (Dubost 1988; Forget 1988; Smythe 1989), some seeds are abandoned or unretrieved, and may survive until community-wide fruit productivity increases. As a consequence, these rodents are effective dispersers in a plant-animal mutualism (Forget 1990b). Given that there is no evidence that removed seeds are not scatterhoarded, and that some cached seeds are not retrieved prior to seedling establishment, it seems hazardous to assume that seed removal is equal to seed predation. The effectiveness of dispersal of large seeds by rodents might depend on fruit and seed features (Foster & Janson 1985; Janson 1983; Sabatier 1983, 1985), on the community-wide fruit availability (Janzen 1971) and on germinated seed features (germination timing and nutrient rewarding from cotyledons) (Forget 1990a, 1990b). These ecological characteristics of rodent-consumed plant species may also influence the degree of competition among terrestrial and arboreal rodents (Smythe 1986; see also Kiltie 1981).

Vandermeer (1979) and Vandermeer *et al.* (1979) documented seed removal of *Welfia georgii* fruits and seeds (see also Schupp & Frost 1989) by both nocturnal and diurnal rodents. Only *Dasyprocta punctata* was observed to cache seeds in the field (Vandermeer *et al.* 1979). Although seed-removal was more important by night than by day, and despite evidence of seed dispersal by captive nocturnal rodents, Vandermeer (1979) concluded that these animals acted exclusively as seed-predators in the field because of the probable low survival of cached seeds. Still, Vandermeer *et al.* (1979) stated they had "no information on the fate of removed seeds (some will be eaten, others buried)" in the field.

In French Guiana, Sist (1989a, 1989b) studied reproduction and recruitment of several palm species, and showed that the pattern of offspring distribution was related to seed disperser behavior. He considered the distribution of *Astrocaryum paramaca* seedlings as the consequence of terrestrial scatterhoarding by the diurnal squirrel (*Sciurus aestuans*) (Sist 1989b). Nocturnal spiny rats (*Proechimys* sp.) acted only as seed predators. Although both animals were seen carrying the seeds from the parent palm, the fates of removed seeds by both

groups of rodents was unknown.

This study describes removal, predation and dispersal of *A. paramaca* seeds by the nocturnal *Proechimys* spp. and the diurnal *M. exilis*. The data represent the first evidence of *Proechimys* scatterhoarding behavior. I discuss the adaptation and the ecological significance of foraging and feeding behavior of *Proechimys* spp., and compare it with *M. exilis* in terms of food availability during and after the *A. paramaca* fruiting season.

### STUDY AREA

The study was performed at the Paracou field station (5° 15' N; 52° 55' W) near Sinnamary, French Guiana. The vegetation type at Paracou is a mature tropical rain forest. Annual mean rainfall is 2870 mm. A long rainy season lasts from December to July, and the dry season occurs between August and November. A decrease in rainfall may occur in February, March or April, but it is irregular and does not correspond to a true dry season. Mean air temperature is 26° C, and mean moisture ranges from 80% to 90%.

### MATERIALS AND METHODS

#### *The palm*

*A. paramaca* is a common acaulescent palm growing in seasonally inundated forests (Sist 1989a, 1989b). Flowering is annual and peaks in November, at the end of the dry season. Fruiting occurs in March-April during the wet season and palms produce one to three infructescences, each averaging 93 fruits. Mature fruits are ovoid, spiny and orange, measure 3.0-4.0 cm x 1.5-2.0 cm, and weigh 4.0-6.0 g. Ripe fruits usually split irregularly, exposing the yellow starchy flesh surrounding the endocarp. Seeds are globular with a coconut-like endosperm. Average seed size and weight are 2.6 x 1.6 cm and 3.8 g, respectively. Once on the ground, the seeds are removed from the neighborhood of the parent tree, being eaten or dispersed by rodents. Seeds are infested by a bruchid (*Pachymerus* sp.); parasitism occurs on the parent during fruit maturation, and the grub penetrates the endocarp before fruit ripening (P.-M. Forget pers. obs.).

#### *Palm stand*

Beginning February 1989, I studied a population of nine *A. paramaca* on a >2500 m<sup>2</sup> area (Fig. 1) near a creek beside the Paracou field camp. The canopy above the *A. paramaca* stands was closed. One palm (H) did not bear fruit in 1989 and another (I) had its infructescence broken by a treefall. Palm A bore three infructescences, B, C and D two, and the other palms only one. Fruit maturation in *A. paramaca* spread from February through May, with a peak between mid-April and early May (Fig. 2). I have done preliminary experiments using seeds from the first infructescences, from palm A (A1 and A2) in February and early March.

#### *Animal behavior*

I observed rodents from a ground-level observatory overhanging the creek area and all palms except palm B (Fig. 1). Observations were supplemented by data on rodent behavior, i.e. seasonal home range, preferred habitats, daily movements, distances traveled, diet, food habits and feeding behavior.

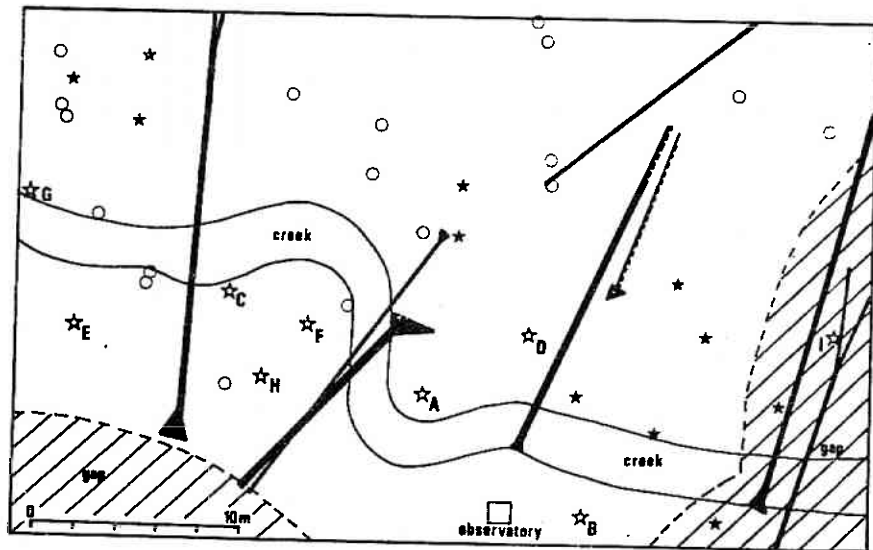


Fig. 1. Study area with locations of adult (empty stars) and juvenile (black stars) *A. paramaca* palms in 1989 at Paracou, French Guiana. Circles: trees more than 20 cm in dbh. Black strips are fallen trees.

#### Nocturnal rodent behavior

I made some observations at early hours of the night and just before sunrise. I captured a *Proechimys* sp. (probably *P. cuvieri*, the most common species, Guillotin 1982a, G. Dubost, pers. comm.) at a distance more than 100 m from the study area. I kept the rodent in a 2.0 x 2.0 x 0.7 m cage and fed it with *A. paramaca* thread-marked seeds (see seed dispersal experiments) mixed with corn, coconuts and native seeds (e.g. *Moronobea coccinea* (Clusiaceae), *Hymenaea courbaril* (Caesalpinaceae)). I covered the cage ground with leaves, branches and logs: piles of leaves were set at the base of a small palm and at three corners of the cage. I set two artificial burrows, one with a *Jessenia* palm sheath that served as the diurnal site, and a shaded tomahawk trap that served as nocturnal feeding site. All objects (leave piles, logs, burrows) were adjusted in order to give different opportunities for food hoarding.

#### Diurnal rodent behavior

I regularly censused rodents between 0600 h and 0900-1000 h, and between 1700-1830 h, during 6 days in mid-April, and irregularly during the entire fruiting period.

#### Seed-removal rate

In order to collect "naturally" ripening fruits and seeds at each palm, I artificially bent the infructescences over one 1 sq. m trap set at 1-1.5 m above the ground. This method prevented seed removal from the trap by terrestrial or arboreal rodents. Fruits and seeds falling into the

traps were censused twice a day : before dawn (0600-0630 h) and after sunset (1900-1930 h). At each census, I placed seeds on the ground under the trap, and I counted the fruits remaining on the ground. I studied seed removal rate from early April through mid-May.

#### *Seed-dispersal experiments*

I did experiments at the base of palm D by baiting the site with marked seeds that were collected at palm B (first experiment), at palm D (second experiment) and at another palm outside the study area (third experiment) starting in mid-March, mid-April, and mid-May, respectively. By mid-May, I stopped the seed-removal study, and seeds were only available under palm D. Each experiment coincided with three different periods of fruit production, e.g. the beginning, the peak and the end of the palm-community fruiting. I marked seeds with pulp with a 60 cm long white nylon thread passing through a hole 1.5 mm in diameter drilled through the endocarp. For the first and second experiments, I followed the census method described for seed removal rate. During the third experiment, I placed one set of 20 seeds on the ground, and I replaced it by another set of 20 seeds when all previous seeds had been removed. I used different knot codes for each day and night period. I searched for threads of removed seeds on the ground at noon at distances up to 25 m from palm D. I numbered the retrieved caches and the sites where seeds were found gnawed with a numbered plastic label fixed on the ground with a metal stake, and I mapped them at the end of the experiment. I censused caches in mid-April, mid-May and mid-June during the wet season, when fruit production community-wide decreases, and in mid-October at the end of the period of food scarcity during the dry season.

## RESULTS

### *Animal behavior*

#### *Nocturnal rodents*

Despite the use of a head-lamp, I could not observe easily the nocturnal rodents from the observatory. However, once before dawn, I saw a *Proechimys* sp. foraging actively at the base of palm D and removing the thread-marked seeds. The animal removed the pulp while sitting on the ground or on the nearest log, and then disappeared with the seed in its mouth. It came back very quickly and showed the same behavior until all seeds had been removed. Immediately after daylight, I searched for the removed seeds, which were always scatterhoarded (see seed-dispersal experiment). The captive *Proechimys* sp. showed the same behavior, and scatterhoarded palm and other seeds by caching them beside the objects placed on the ground and in the pile of leaves. Larderhoarding (see Vander Wall 1990) of each food was also observed, probably because of the restricted area of the cage and the limited number of suitable hoarding places. However, I never saw *Proechimys* sp. digging the ground with its forepaw as does *M. exilis*; the captive spiny rat cached seeds only by pushing them under the litter with its nose and covering them with additional leaves. Seeds were also hoarded in the artificial burrow and in the nocturnal feeding site.

### *Diurnal rodents*

Both terrestrial and arboreal rodents were observed foraging on the study plot. *M. exilis* was the main diurnal visitor. It came regularly each day during the whole fruiting period to the base of the palms. One *M. exilis* was observed both eating and scatterhoarding seeds very close (1-2 m) to the palms. Sometimes, it carried seeds away out of view, and the time spent before the rodent returned to the palm was variable (1-2 mn up to 10 mn). *S. aestuans* was seen three times during the regular census and not afterwards, moving on lianas, branches and small trees. *S. aestuans* never foraged on the ground even when seeds were available beneath the palm. Once, a squirrel climbed an *Attalea* palm leaf and came very close to the infructescence but did not remove any seeds.

### *Seed-removal rate*

To show differences between sites, I summarized results for each palm (Table 1). These include those of the second seed dispersal experiment at Palm D but not the first, which was done before the other palms dropped their seeds (see seed-dispersal results). The order of the palm infructescences follows the timing of their ripening from April through May. Because the ripening of two infructescences of palm B overlapped, they were considered as one infructescence. No seeds had been removed during the day at either palm D2 or G1. Short-term results were thus grouped. In Table 1 the number of seeds placed on the ground exceeded the number of seeds collected in trap. Indeed, when seed removal rate is not 100% each night or each day, the effect of seeds remaining at the bait was thus added to the new seeds collected: if 10 seeds are placed on the ground each day, and 5 only are removed each day, after two days, the total number offered is 25 ( $10 + [10 + 5]$ ) while only 20 seeds were produced. Therefore, two kinds of seed removal rates are expressed. SRRI is the ratio between the number of seeds removed vs. the total number of seeds offered per period. This rate is a rough estimate of the frequency of rodents at each palm; if both nocturnal and diurnal rodents were very frequently visiting a given palm, then SRRI might reach 100% both by night and by day (almost the case of palms C and E). SRR 2 is the ratio between the number of seeds removed per period vs. the number of seeds produced by the infructescence. This rate evaluates the proportion of seed removal at each palm that is due to each group of rodents; SRR2 by night adds with SRR2 by day equal 100%.

There were large differences in seed removal between day and night, as well as between palms (Table 1). Except for palm E, the nocturnal rodents visited each palm more frequently and removed more seeds than the diurnal rodents (Table 1). For the whole area, nocturnal rodents removed 3.3 times more seeds than did diurnals, and consequently SRRI and SRR 2 were 2.5 and 3.2 times greater, respectively, by night than by day (Table 1).

### *Seed-dispersal experiments*

i) *First experiment: early fruiting (mid-March)*. Of 106 seeds produced by infructescence B1, only one seed was removed during the day and subsequently retrieved. During ten nights, of  $20.2 \pm 10.6$  seeds (range 1-35) placed at the base of palm D,  $10.5 \pm 10.9$  seeds (range 0-33) were removed per night. SRRI and SRR2 for seeds removed at night were 52% (105 vs. 202) and 99% (105 vs. 106), respectively. 68.5% of the seeds (N = 105) had been cached, and 6.7% were eaten (thread on the ground with a part of the endocarp still attached). Each cache contained only one seed. When all seeds were removed from the baiting area, I observed that the

TABLE 1. Nocturnal and diurnal seed removal of *Astrocaryum paramaca* in French Guiana.

Palm a (No. seeds) b	Night/ Day N/D	No. of nights or days	Seeds placed on the ground			Removed seeds			SRR1 (%) e	SRR2 (%) f
			Mean ± 1 SD	range	Total	Mean ± 1 SD	range	Total		
A3 (151)	N	15	14.6 ± 13.3	1-45	219	7.5 ± 9.6	0-32 c	113	51.6	74.8
	D	14	11.6 ± 9.2	1-28	162	2.7 ± 0.2	0-7	38	23.5	25.2
B2 (131)	N	17	12.3 ± 6.9	1-22	210	7.5 ± 7.1	0-20	128	60.9	97.7
	D	17	9.6 ± 6.0	1-19	155			3d	15.8	2.3
C (134)	N	23	3.8 ± 2.9	1-11	88	3.5 ± 3.1	0-11	81	92.1	60.4
	D	26	3.0 ± 2.1	1-7	79	2.0 ± 2.1	0-7	53	67.1	39.6
D1 (59)	N	15	5.5 ± 3.8	1-12	83	3.5 ± 2.9	0-9	53	63.9	89.8
	D	13	3.7 ± 2.5	1-9	48	0.5 ± 0.8	0-2	6	12.5	10.2
E (26)	N	7	1.1 ± 0.4	1-2	8	0.9 ± 0.7	0-2	6	75.0	23.1
	D	9	2.4 ± 1.4	1-5	22	2.2 ± 1.6	1-5	20	90.9	76.9
F (60)	N	8	5.4 ± 3.5	1-12	43	4.8 ± 4.0	0-12	38	88.4	63.3
	D	10	4.9 ± 4.1	1-13	49	2.2 ± 2.3	0-7	22	44.9	36.7
D2G (34)	N	7	9.4 ± 7.3	13-25	66	4.9 ± 0.9	3-25	34	51.5	100.0
	D	6	8.2 ± 6.6	2-21	49	0	0	0	0	0
Total (595)	N	38	18.8 ± 15.0	1-68	715	11.9 ± 10.7	0-39	453	63.3	76.1
	D	39	14.4 ± 11.4	1-47	561	3.6 ± 3.4	0-11	142	25.3	23.9

a. Palm with # of infructescences.

b. Number of seeds collected in the trap.

c. The creek was flooded one night and is responsible for part of seed removal.

d. Diurnal seed removal occurred during only one day when 19 seeds were initially on the ground.

e. SRR1 is the ratio between the total number of removed seeds and the total number of seeds placed on the ground by night or by day.

f. SRR2 is the ratio between the total number of removed seeds by night or by day and the total number of seeds produced by the infructescences.

entrances of natural cavities (Fig. 2) were used by animals to eat or store seeds. I found in those cavities many destroyed, unmarked and marked endocarps, threads, and two entire marked seeds. The number of caches includes some that were discovered later, when no seeds were available at the palm. I assume that these caches comprised seeds previously larderhoarded in burrows and cavities used as feeding sites, and then scatterhoarded later.

Of cached seeds, 45.8% were between 5 m and 10 m from the original set location (Fig. 3). Some seeds were cached at the base of the palm, and others up to 14.5 m distant from the base. Cached seeds were above the ground, and were easily extracted from the litter by pulling on the thread. No seeds appeared to be buried under the ground.

During the wet season, 68.1% (N=49), 33.3% (N=24) and 12.5% (N=9) of cached seeds remained unremoved after one, two and three months respectively. Seven months after the beginning of the experiment, only 2.7% (N=2) of cached seeds remained alive, one germinated and sprouted leaves. These seeds were situated close to the log beside the palm D (Fig. 3).

ii) *Second experiment: peak of fruiting (mid-April)*. SRR1 and SRR2 were 5.1 and 8.8

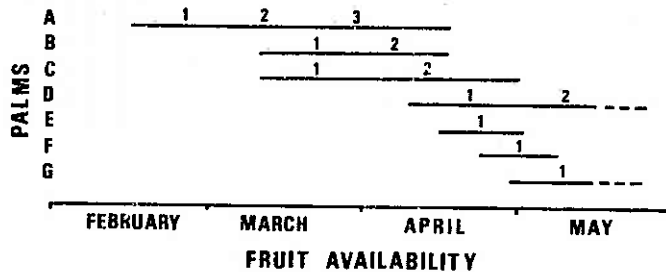


Fig. 2. Period of fruit availability at each *A. paramaca* of the palm-community studied from February through May 1989. Dashed lines indicate that the study was stopped at mid-May.

times greater by night than by day, respectively (Table 1), but none of the seeds were cached in the field. This seed removal represents both seed-predation and hoarding in burrows and in arboreal caches, by nocturnal and diurnal rodents, respectively.

iii) *Third experiment: end of fruiting (mid-May)*: All seeds (40) disappeared the first night after being placed. Twenty-one of them were cached (Fig. 3), most more than 10 m from the palm; the proportion of seeds cached at different distances from the palm are not significantly different ( $X^2$  ns) from that of the first experiment. Ninety percent of seeds remained cached by mid-June, but all were removed by October.

## DISCUSSION

### *The dispersers of A. paramaca seeds*

Removal of *A. paramaca* seeds at Paracou is attributable to terrestrial and arboreal rodents such as *P. Guyannensis*, *P. cuvieri*, *M. exilis*, *D. leporina*, *S. aestuans*, and probably also to other small rodents; each acts as predator as well as disperser.

### *Nocturnal rodents*

Before this study, no evidence had been reported for scatterhoarding behaviour of *Proechimys* spp. in the field. This animal was only known and assumed to hoard food in den sites and in burrows, both in captivity as well as in the field (Emmons 1982; Fleming 1971, Forget 1988, 1990b; Guillotin 1982b; Maliniak & Eisenberg 1971; Symthe 1970). Hence, nocturnal seed removal had always been linked with seed predation. Here, *A. paramaca* seeds were removed and dispersed by *Proechimys* spp. which prey upon cached seeds during several months.

### *Diurnal rodents*

In contrast with Sist's (1989a) observations during the dry season, *S. aestuans* were apparently not involved in removal of *A. paramaca* seeds during the wet season. The related



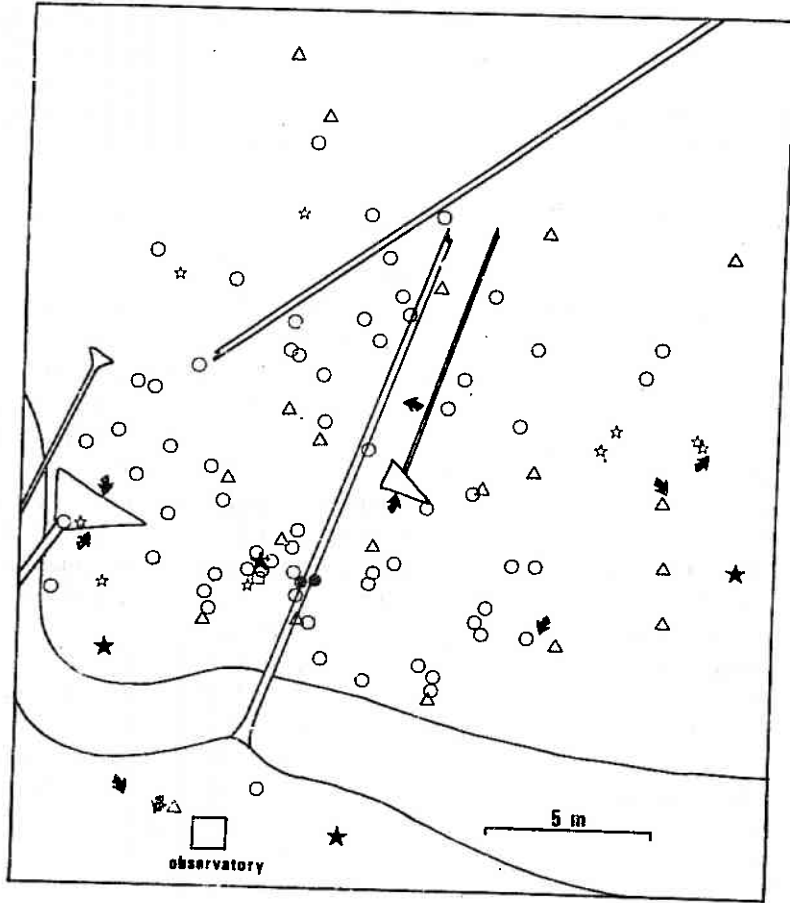


Fig. 3. Scatterhoarding and predation of *A. paramaca* seeds by rodents around an experimental bait (square) set at the base of palm D. Black stars: location of adult palms. Destination of removed seeds: circle: cached seed and star: gnawed seed during the first experiment (mid-March); triangle: cached seed during the third experiment (mid-May); full circles: abandoned seeds in October 1989. Arrow: location of burrow entrances and den sites used by nocturnal rodents during the experiments. Strips are fallen trees.

species of Central America, *S. granatensis*, can be regularly observed on the ground searching for food (Heaney & Thorington 1978; Glanz *et al.* 1982; *pers. obs.*). In contrast, *S. aestuans* rarely forages on the ground in French Guiana. The importance of *S. aestuans* as a potential seed disperser of *A. paramaca* during the wet season may be considered to be minimal unless it is demonstrated that *S. aestuans* regularly make terrestrial caches like *S. granatensis* in Panama (Heaney & Thorington 1978; *pers. obs.*).

*D. leporina* was not observed at the creek site though it is present at Paracou mature forest.

## SCATTERHOARDING OF PALM SEEDS *PROECHIMYS*

*M. exilis* forages near dense sites (tree falls, dense undergrowth, lianas) more often than does *D. leporina*, and shows a clear preference for the areas near the water, whereas *D. leporina* prefers to be inland (Dubost 1988). Nonetheless, *D. leporina* often forages in seasonally inundated forests (Dubost 1988), and where *A. paramaca* palms are abundant (Sist 1989a, 1989b).

The rate of nocturnal seed removal probably varies from site to site, and may be a function of the physical features of habitat as well as of the frequency of visits by caviomorph rodents. During this study, seed removal and dispersal of *A. paramaca* seeds was primarily by night by *Proechimys* spp., and by day by *M. exilis*.

### *Seed removal rate and foraging behaviour*

The *A. paramaca* fruiting period lasts several months, at the same time that forest community-wide fruiting is maximum in the forest (Sabatier 1985; Sist 1989b). During experiments, high seed-removal rates (up to 100%) at one palm alternated with lower (0-10%) seed-removal rates, both by night and by day. It is possible that rate of seed dispersal also varies from palm to palm. Rodents did not often visit the fruiting palms each day; they ate and dispersed seeds when they passed by the area at intervals of several days. From March through May, rodents can feed on other alternative resources available on their home-range, and can thus be satiated. As a consequence, they do not forage exclusively at *A. paramaca*. Also, this range of seed removal rate may be due to the features of the microhabitat that is surrounding each palm, which may or may not be favourable for foraging by a given rodents. For example, because of the predator risk, an acouchy may visit less frequently a palm growing in a very open understory lacking microsites for hiding such as logs.

Size differs between *Proechimys cuvieri* and *M. exilis* (160-500 g vs. 1,000-1,450 g, respectively; Guillotin 1982a; Dubost 1988). Their home-ranges are similar in size during the wet season (8431/3145 m<sup>2</sup> for male/female of *P. cuvieri* vs. 6500-12,000 m<sup>2</sup> for both sexes of *M. exilis*). Nevertheless, differences in seed-removal rates can be understood by the differences and changes in foraging behaviours. Scatterhoarding (present study) and feeding (Guillotin 1982b) behaviors of *P. cuvieri* differ from those of *M. exilis* (Morris 1962; Forget 1988, 1990b). The former forages actively on a portion of its home-range, and travels short distances per night in search of food (Guillotin 1982b). Seed removal during the night is likely to increase when several species use the same area (see Emmons 1982). In the latter species, both sexes use the whole home range each day, travelling longer distances than *P. cuvieri*, and staying for shorter time periods at the same place (*pers. obs.*) during the period of activity (Dubost 1988). This may explain why, during the *A. paramaca* fruiting period, seed removal was higher by nocturnal than by diurnal rodents.

*A. paramaca* seed removal rates are consistent with results of Vandermeer *et al.* (1979), and confirm the high seed removal rate by nocturnal rodents. It cannot be concluded that all nocturnal rodents cache seeds throughout the year, and the expression of this behaviour probably changes according to rodent species, plant species, animal or seed size, and community-wide fruit availability (see also Vander Wall 1990).

### *Seed size and hoarding behaviour*

*P. cuvieri* prefers (>40% of the diet) seeds that are 2.0-3.0 cm in diameter and only 10% of

its diet consists of seeds larger than 3.0 cm (Guillotin 1982b). *Proechimys* spp. seems poorly adapted for digging the ground in order to cache seeds as does *M. exilis*. However, at the beginning of community-wide fruit production, *Proechimys* spp. may cache in the litter some small-seeded species (1.0-3.0 cm in length); it often also uses feeding sites to cache, and feeds on cached seeds (and also later germinations, *pers. obs.*) intensively during the wet season. These temporary caches can easily be found by other rodents, particularly by *M. exilis* that forage on the same area by day. Because of their small size, *Proechimys* spp. can also hide in dens and dark sites (under palm leaves, beside tree buttresses) and in natural cavities (holes in ground, hollow logs, see Emmons 1982, for more details on use of these sites) to eat seeds. *M. exilis* mostly feeds in the open and is therefore less protected from terrestrial (but not arboreal) predators, although it can flee to the nearest hollow log (Dubost 1988; *pers. obs.*). As a consequence, *P. cuvieri* spends a longer time than *M. exilis* in an area where it stores food, and it seems that it is very efficient in retrieving cached seeds.

When very large-seeded species (>3.0 cm) such as *Carapa procera*, *Vouacapoua americana* and *M. coccinea* fruit from March through June (cf. Sabatier 1985; Forget 1988, 1990a, 1990b, 1991), *P. cuvieri* shifts to this new nutrient-rich food. Seed weight (> 10g) may prevent *Proechimys* spp. from carrying large seeds long distances from the seed source to safe feeding sites. *P. cuvieri* may eat part of the seed and then carry the rest to a den site or a burrow. *P. cuvieri* rarely hoards in a burrow (Guillotin 1982b). Some large-seeded species are cached under the litter close to the tree (e.g. *M. coccinea*) but, as in *A. paramaca*, these sites would not be well protected against other competitors and there is high post-dispersal predation (*pers. obs.*) At least part of the diet of *P. cuvieri* consists of insects (9% and 32% of the total diet during the wet and dry season, respectively; Guillotin 1982b), whereas *M. exilis* may maintain a granivorous diet by feeding on long-term seed caches.

In a previous study of *Vouacapoua americana* (Forget 1990b) some seeds were buried and cached in a manner similar to that described in this study. Although most seeds disappeared the first day, some remained until night, and then disappeared. It is possible that some of the cached *V. americana* seeds were hoarded by *Proechimys* spp. Nevertheless *Proechimys* spp. are more efficient seed-removers for *A. paramaca* than for *V. americana*, and vice versa for *M. exilis*.

#### *Consequences of scatterhoarding on palm regeneration*

In contrast to other large-seeded species (Forget 1990a, 1990b, 1991 *pers. obs.*) for which burying by *M. exilis* and *D. leporina* is essential for germination survival, *A. paramaca* seeds under the litter may germinate despite the high post-dispersal predation by *proechimys* spp. (and probably other rodents). *Proechimys* spp. may improve seedling establishment by facilitating rooting. Some germinations from caches may be protected from rodents which feed on young high-nutrient radicles and persistent cotyledons during the period of fruit scarcity. The cache of *M. exilis* (buried seed) might be more effective in this respect. Finally, seedlings may arise from caches of both rodents. Unfortunately, because of the low seed-dispersal rate of diurnal rodents, it was not possible to compare the proportion of dispersal and seedling establishment due to each group of rodents. It was thus not possible to determine whether the rate of seed-removal is correlated with that of seed-dispersal. One may conclude, however, that both *Proechimys* spp. and *M. exilis* are reliable dispersers of *A. paramaca*

palm.

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#### Erratum

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