

Seed-dispersal of *Vouacapoua americana* (Caesalpinaceae) by caviomorph rodents in French Guiana

PIERRE-MICHEL FORGET

*Université Pierre et Marie Curie (Paris 6), Laboratoire de Botanique
Tropicale, 12 rue Cuvier, 75005 Paris, France*

ABSTRACT. A possible mutualistic dispersal system between a large-seeded tree of French Guiana, *Vouacapoua americana* (Caesalpinaceae), and caviomorph rodents, *Myoprocta exilis* and *Dasyprocta leporina*, is described. Mast fruiting of *Vouacapoua* at the beginning of the wet season coincides with scatter-hoarding seed dispersal. During the wet season, almost 100% of marked seeds on three sites were removed: nearly 70% were buried and the rest were eaten by mammals. Unburied seeds were attacked by insects and/or lost their ability to germinate. Rodents preferred ungerminated seeds, and had no interest in germinated seeds. Seeds were buried individually near natural objects such as palms, branches, logs, lianas, roots and trees. After predation by rodents, seedling distribution did not differ from seed distribution. Most seeds were transported less than 5 m from the feeding plots but some were carried as far as 22.4 m. Between 40 and 85% of dispersed seeds were retrieved during the following month by rodents and eaten. The disinterest of caviomorph rodents in germinated seeds, because of rapid exhaustion of endosperm reserves, prevents feeding from hoarded *Vouacapoua* during the long dry season when resources are scarce. Seedlings emerging from forgotten or abandoned cached seeds appear to increase the recruitment of *Vouacapoua americana*.

KEY WORDS: caviomorph rodents, mutualism, *Myoprocta exilis*, scatter-hoarding, seed-dispersal, tropical rain forest, *Vouacapoua americana*.

INTRODUCTION

In Neotropical forests, seed dispersal and recruitment of some plants depends to a large extent on large caviomorph rodents such as acouchies and agoutis. In French Guiana, *Myoprocta exilis* (Wagler 1831) and *Dasyprocta leporina* (L. 1758) (Dasyproctidae) co-occur in undisturbed forest (Husson 1978) and feed on fruits and seeds (Dubost 1988). These animals make caches, each containing one fruit or seed, that are located around a parent tree. This phenomenon, 'scatter-hoarding', contrasts with 'larder-hoarding' by other rodents which amass many fruits or seeds in the same cache (Morris 1962). According to Janzen (1969, 1970), survival of seeds and seedlings around the parent tree should be closely correlated with fruit type, predators, dispersal agents and dispersal distance.

Present address: Smithsonian Tropical Research Institute, APO Miami 34002, USA and Laboratoire d'Ecologie Générale, Muséum National d'Histoire Naturelle, 4 Avenue du Petit Château, 91800 Brunoy, France.

Hoarding has been studied most in the temperate zone but in the tropics we do not know its impact on forest dynamics. Two studies have been reported: the first by Morris (1962) on captive acouchies (*Myoprocta pratti*) fed with biscuits, and the second on agoutis (*Dasyprocta punctata*) fed with *Hymenaea* fruits in a dry forest in Costa Rica. In French Guiana, Sabatier (1983) described the scatter-hoarding behaviour of a young captive *Myoprocta exilis* (ex *M. acouchi*). Despite many accounts in the literature on seed predation and scatter-hoarding by these rodents, many features are still unknown, such as (a) the proportion of seeds eaten (pre- and post-dispersal), (b) the dispersal potential (distance from the seed source), (c) the survival of dispersed seeds (post-dispersal mortality) and (d) the consequences of seed dispersal on recruitment (seed germination and seedling establishment). The dispersal of *Vouacapoua americana* Aublet (Caesalpiniaceae) seeds by caviomorph rodents was investigated in French Guiana as part of a study on the recruitment of this species.

NATURAL HISTORY BACKGROUND

Vouacapoua americana is a common large tree of French Guiana, with a distribution from Brazil to Venezuela. Fruiting is characteristic of 'mast-fruited' as described by Janzen (1974) with occasional individuals outside the general synchrony (Sabatier 1983, 1985). Flowering occurs in February–March (the short dry season), and fruiting during April, May and June (the long wet season).

The fruits are yellow to orange-brown pods (Figure 1a) measuring $7.2 \pm 0.1 \times 4.0 \pm 0.1$ cm (range: 6.2–7.4 \times 3.1–5.0 cm; N = 30), and weigh 48.2 ± 2.2 g (range: 27.0–57.0 g; N = 30). Each contains one or two seeds; the seeds are brown, odoriferous and pear-shaped with a hard endocarp. Average seed size is $4.9 \pm 0.1 \times 3.4 \pm 0.1$ cm (range 4.2–5.5 \times 3.1–3.8 cm; N = 30), and mean weight is 32.6 ± 1.8 g (range: 17.0–40.0 g; N = 30). Seed production ranges from 120–3200 per tree (N = 10) (Sabatier 1983). At maturity, the heavy pods and large seeds are released and fall to the ground, after which caviomorph rodents may carry away and bury the seeds (Sabatier 1983). In 1980, Sabatier (1983) estimated that for nine trees, 15 days after fruiting ended, the percentage of seeds that had disappeared was 35.7 (range: 4.0–82.5%), and that predispersal predation of seeds by rodents was 5% (range: 2.0–7.5%); for one tree he noticed that 88.5% of teeth marks on the pods belonged to *Myoprocta exilis* and 11.5% to *Proechimys cuvieri*. Spiny rats (*Proechimys* spp.) larder-hoard *Vouacapoua* seeds in their burrows, (Guillotin 1981) but there was no evidence that they scatter-hoard them.

METHODS

The study site

The study was conducted in French Guiana from March to May 1987 at the Ecological Station of the Muséum National d'Histoire Naturelle (Arataye-

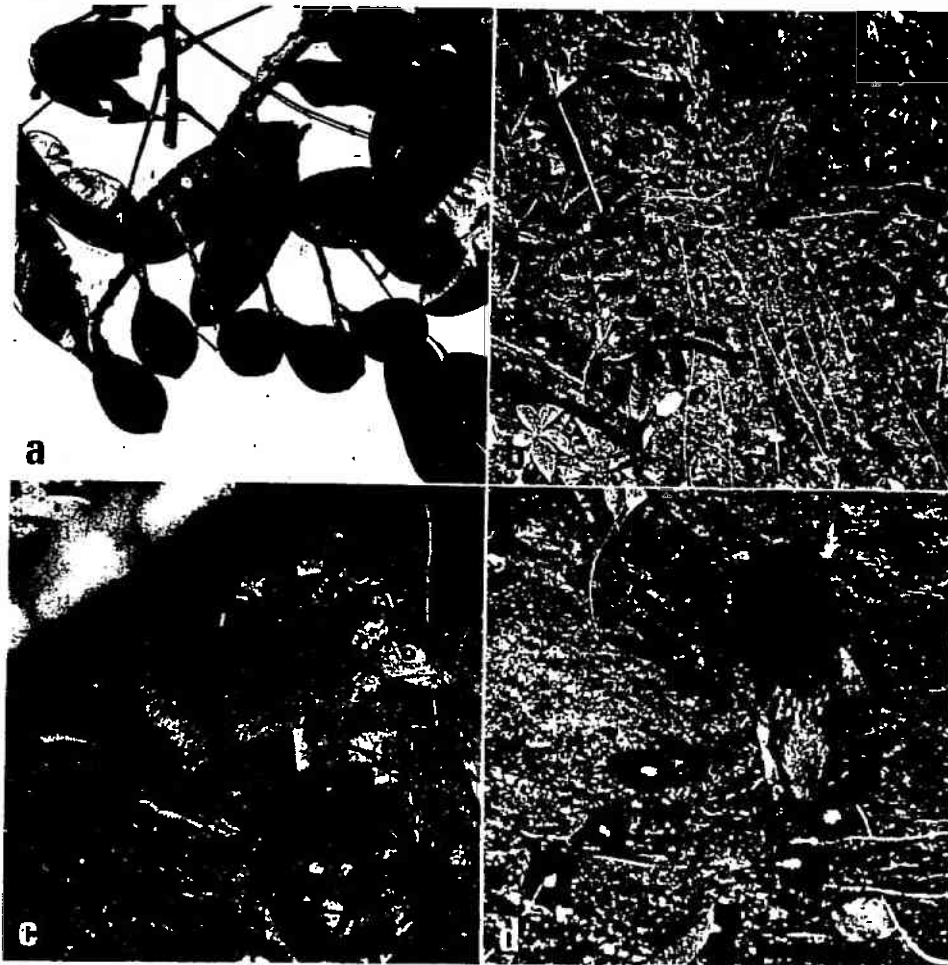


Figure 1. a: Mature *Vouacapoua* fruits; b: Feeding plots with 25 seeds marked with thread 50–60 cm long; c: Young acouchy *Myoprocta exilis*; d: Young acouchy taking a seed of *Vouacapoua*.

Nourague Camp) 8 km distant from Pararé waterfalls ($4^{\circ} 02' N$, $52^{\circ} 42' W$). No rainfall data are available for this station but according to the atlas of French Guiana it is likely to be similar to that of ECEREX station ($5^{\circ} 30' N$, $53^{\circ} 00' W$) where the mean annual rainfall is 3196 mm (1977–1986) with a wet season from September through November. Occasionally, there is a decrease in rainfall (short dry season) during February, March or April and the wet period is divided into a short and a long wet season. At ECEREX site, the fruiting season occurs from November to August with maximum fruit production in March–April (Sabatier 1985).

Seed germination

On 29 March 1987, 60 seeds which were free of insect infestation were buried or placed on the ground and protected with nets from seed predators

in each of three locations (1) in the centre of a big gap (200 m² *sensu* Brokaw 1982), (2) on the edge of this gap and (3) in the understory near a parent tree crown.

Seed predation and seed dispersal

Seed predation and seed removal by terrestrial mammals were studied during the *Vouacapoua* fruiting period, starting 25 March, by making two feeding plots of 25 seeds each near four fruiting trees. On 30 March two further feeding plots, each with four sets of 25 seeds, were established 50 m from the nearest *Vouacapoua* tree, one at the edge of a creek and the other on top of a ridge. These plots were checked 15 times over a period of one month. Observations in the field permitted identification of some of the seed predators (insects and rodents). Otherwise germinated seeds that were infested by insect grubs were kept in a plastic box in order to identify the adults emerging from the seeds.

Seed caching and retrieval were studied at the end of the *Vouacapoua* fruiting period, during May 1987, by preparing feeding plots at dawn (06.00–06.30 h) with seeds, each marked with a thin white thread 50–60 cm long passing through it (Figure 1b), at three sites on top of the ridge 30–50 m apart and 200 m from the nearest fruiting *Vouacapoua*. Knots, coded for each plot, were made in the threads to enable the origin of removed or cached seeds to be traced. At site 1, 25 seeds were positioned on 3, 5 and 6 May; at site 2, two plots of 25 seeds were made on 4 May and at site 3, two plots of 30 seeds were made on 9 May. On subsequent days, removed seeds were relocated during the morning (between 09.00/10.00 h and midday) when rodents are less active. The distance between the cache (indicated by the thread coming out of the ground), or eaten seed (thread on the ground), and origin were measured. Buried seeds were marked with a 16 × 1 cm label and regularly observed until 28 May (about 3 weeks).

On 3 May, at site 1, the removal rate of 25 ungerminated seeds was compared with that of 25 germinated marked seeds.

During these experiments the diurnal consumer–dispersers of *Vouacapoua* seeds were observed from an elevated hide 2 m above the forest floor at sites 1 and 2.

RESULTS

Seed germination

Vouacapoua seeds germinated (emergence of the radicle) rapidly when they were buried under 3–5 cm of litter; the germination was 100% (N = 30) after six days in each site (gap edge, gap centre and understory). When seed were left on the ground the germination after 18 days was 60% in the understory, 23.4% at the edge of the gap, and 0% in the centre of the gap. After one month, 100% of the unburied seeds in the understory had germinated. Plumules of buried seeds appeared after 2–3 weeks, and seedlings were completely formed 6–8 weeks after sowing.

Seed predation and seed removal

During the *Vouacapoua* fruiting period, the seed removal (predation and dispersal/hoarding) rate was low, both near the trees and on the edge of the creek after seven days, and one month (Table 1, Figure 2). In contrast, on the ridge the removal rate increased after seven days reaching 96% after one month (Table 1, Figure 2). On this site no seeds germinated, whereas on the other two sites all undispersed seed germinated. Both agoutis and acouchies were observed eating seeds on the feeding plots. It is well known that peccaries (*Tayassu tajacu* and *T. pecari*) like *Vouacapoua* seeds, but teeth marks of these animals were never observed on the pods during the fruiting period. On the ground, unidentified ants were seen on the unburied seeds; they emptied the cotyledon reserves after making a hole in the seed coat. Beetle grubs (Curculionidae, Hylobininae, Cryptorhynchinae, Scolytidae, Nitidulidae) infested germinated seeds.

Table 1. *Vouacapoua* seed removal rate (%) after seven days and after one month under four fruiting trees (N = 200) and at two sites 50 m distant from the nearest fruiting tree: on the edge of a creek (N = 100) and on top of a ridge (N = 100).

	Under fruiting trees	Creek	Ridge
7 days	2.5 (range: 0-6)	11	12
1 month	10.5 (range: 0-34)	21	96

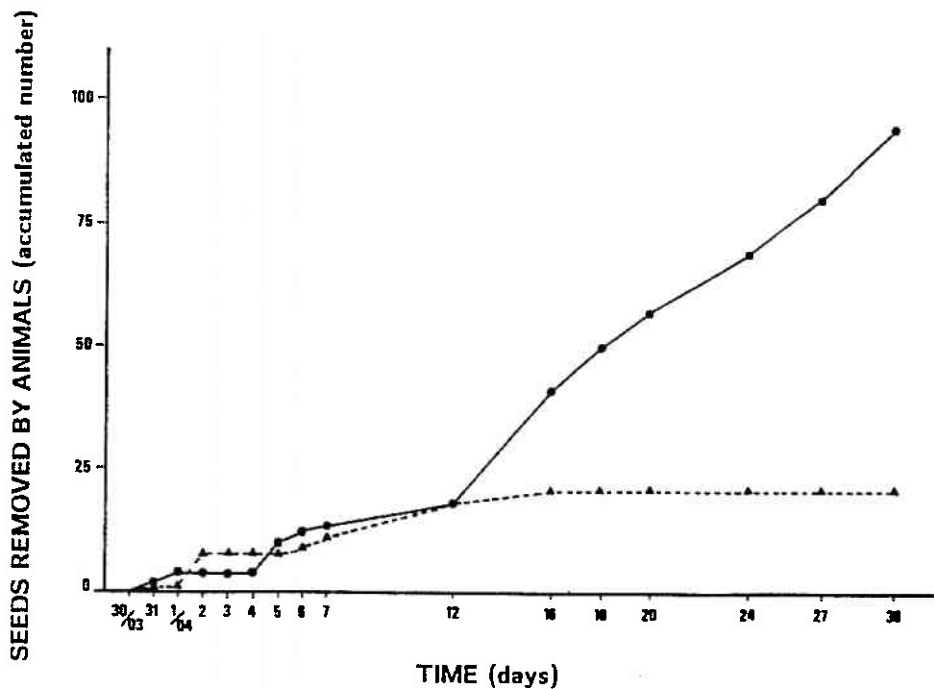


Figure 2. *Vouacapoua* seed removal on the edge of the creek (▲—▲) and at the top of the ridge (●—●) during April 1987; totals of four sets of seeds at each plot.

Table 2. Dispersal and predation of *Vouacapoua* seeds in May 1987 on three ridge-top sites 200 m distant from the nearest fruiting tree. Percentages are of: (a) N; (b) seeds removed by animals; (c) seeds retrieved by researcher; (d) seeds buried by animals.

		Site 1 N = 75		Site 2 N = 50		Site 3 N = 60	
		No.	%	No.	%	No.	%
Removed (animals)	(a)	75	100.0	47	94.0	60	100.0
Retrieved (researcher)	(b)	73	97.3	24	51.0	50	83.3
Buried	(c)	52	71.2	16	66.7	35	70.0
Gnawed <i>in situ</i>	(c)	21	28.8	8	33.3	15	30.0
Dug up (uprooted)	(d)	21	40.4	8	50.0	30	85.7
Total destroyed	(b)	44	58.7	39	83.0	55	91.7

On the ridge (sites 1, 2 and 3), where 25 or 30 seeds were placed on the ground at the end of the *Vouacapoua* fruiting period, all or most of the seeds were removed the same morning. The threads did not seem to influence rodent behaviour. After 10 days, only three of the 185 seeds had not been transported, hoarded or gnawed. These three seeds had germinated, after which the radicles had been bitten off and eaten. Ultimately the seed removal reached 100% at sites 1 and 3, and 94% at site 2 (Table 2). Rodents ate or dispersed both insect free and infested seed. Marked seeds were treated differently at each site by the rodents (Table 2, Figure 3). The missing seeds (unretrieved by researcher) were probably carried away by diurnal or nocturnal rodents. Seeds were found up to 22.4 m away from the feeding plots, but most were less than 5 m distant (Figure 3). Some seeds were transported without being buried or gnawed and were hoarded or eaten the next day. Also seeds were observed 30–50 cm apart at the base of the same natural object (see below) but seeds were never seen cached together at the same place.

More than 80% of the seeds were accounted for at sites 1 and 3, but only 51% at site 2. The number of dispersed/buried seeds was, in each case, 2–2.5 times greater than the number of those gnawed before dispersal. In this respect, there was no significant difference between these three sites ($\chi^2 = 0.17$ ns; DF = 2).

On the other hand, the total number of hoarded seeds recovered by animals differed between sites ($\chi^2 = 18.1$; DF = 2; $P < 0.001$), varying from 40.4% (site 1) to 85% (site 3) (Table 2), and from 25% (site 1) to 100% (site 3) for seeds deposited less than 5 m away from the feeding plots (Figure 3). At site 3, 55% of the buried seeds disappeared during the 2–4 days following their dispersal/hoarding, as opposed to only 37% after 15 days at site 1. One of the two experimental feeding plots at site 3 was 3.5 m away from a rodent resting place under a big hollow log with several entrances. The five seeds that remained viable on 28 April originated from the other plot, 9.0 m away from the log. Seeds which rapidly disappeared were buried either around the feeding plots and the pathways used by the animals, or around the log and the resting place entrances. Some of the seeds had acouchy tooth marks on them.

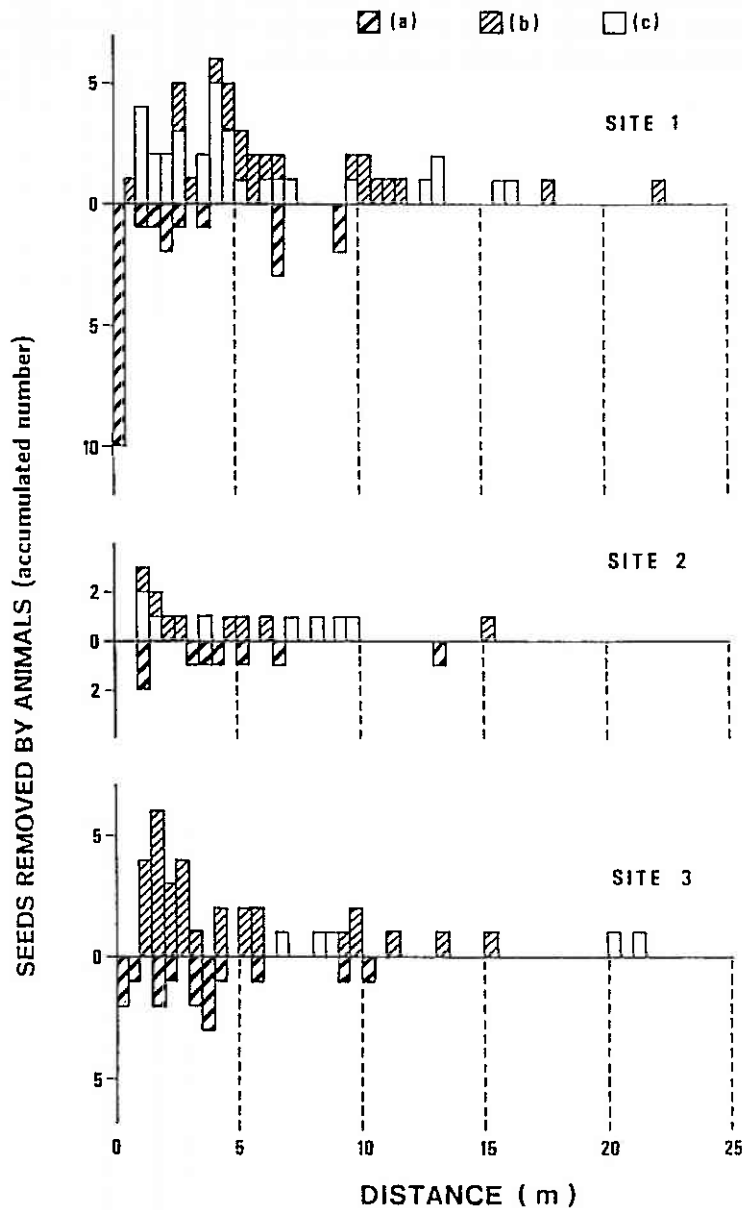


Figure 3. Number of *Vouacapoua* seeds (a) gnawed without being dispersed, (b) dispersed then retrieved (by animals) and (c) dispersed and not retrieved by animals, in relation to the distance from the feeding plots at sites 1 ($N = 73$), 2 ($N = 24$) and 3 ($N = 50$) in May 1987.

In the experiment to compare the removal of ungerminated with germinated seeds, 100% of the ungerminated seeds were removed, whereas only 4% of the germinated seeds were removed, although some radicles were, again, bitten off. By May 1987, no seedlings had been uprooted by the animals.

From the hides (at sites 1 and 2) acouchies (Figure 1c) were the only animals seen to remove seeds from the feeding plots (Figure 1d). At site 2, during

Table 3. Distribution of *Vouacapoua* seeds (N = 103) and seedlings (N = 44) in May 1987 as a function of their proximity (< 50 cm) to natural objects or without particular localization (> 50 cm).

Localization	Seeds		Seedlings	
	N	%	N	%
< 50 cm				
Palms	25	24.3	14	31.8
Branches/logs	18	17.5	10	22.7
Lianas/roots	4	3.9	2	4.5
Trees	13	12.6	5	11.4
Miscellaneous	10	9.7	4	9.1
Subtotal	70	68.0	35	79.5
> 50 cm	33	32.0	9	20.5
Total	103	100.0	44	100.0

15 X 1.5 h periods between 17.00 and 18.30 h acouchies were observed seven times. On occasions, several individuals were seen together.

Distribution and nature of caches

From a total of 103 located seed caches, 68% were less than 50 cm distant from the nearest natural objects (Table 3). These objects included piles of litter at the bases of palms, the bases of trees, dead branches, logs, lianas and exposed roots. Several objects such as large plants (Bromeliaceae and Maranthaceae) or old treefall pits were grouped together as miscellaneous. After post-dispersal predation by rodents, seedling distribution did not differ from seed distribution near these objects ($\chi^2 = 6.39$ ns; DF = 4) (Table 3).

DISCUSSION

Burying of *Vouacapoua* seeds accelerated germination probably because microclimatic features prevent germination of unburied seeds during the short dry season. In March, rodent activity (both predation and dispersal) was very low and was not associated with mast-fruiting of *Vouacapoua*. Because high humidity along the creek probably enhanced seed germination of undispersed seeds, seed removal at the creek site and near the trees was not so high as on the ridge. Conversely, undispersed seeds did not germinate on the ridge, and remained attractive to rodents. Thus seed removal rate progressively increased between mid-April to the end of April and the beginning of May, when there were no more fruits or ungerminated seeds under the trees. Some unburied seeds were desiccated and/or infested by insects. On the ridge, all dispersed and missing seeds must have lost their ability to germinate because no seedlings were found in the following month. Similar results have been obtained during germination studies of large seeds of other species (McHargue & Hartshorn 1983, Sork 1985). Seeds of this kind are called recalcitrant seeds by physiologists (Roberts 1973), and 'sowing' by caviomorph rodents appears to prevent desiccation.

Results of these seed dispersal experiments at the beginning of the long wet season showed a high rodent activity during the usual fruiting peak of large-seeded species (Sabatier 1985). Rodent density, rainfall and fruit productivity could determine the rate of seed removal during the fruiting period. The maximal dispersal distance (22.4 m) is half that recorded by Smythe (1978) and much lower than those observed by Hallwachs (1986) in Costa Rica for agoutis (*Dasyprocta punctata*). Dispersal distances could depend on the dispersing animal, seed size, habitat and the animal's use of its home range. Like Smythe (1978) and Kiltie (1981) I observed many dispersed seeds and seedlings at the base of natural objects, but unlike Kiltie (1981) I did not find a higher post-dispersal predation near these objects, maybe because of the absence of peccaries during the experiments. Furthermore, the frequency of seeds near these structures is probably a function of their density around the feeding plots and it is possible that retrieval of seeds by rodents is governed by chance in an area where the animals are searching for food, seeds finally being found by means of olfactory cues (Murie 1977). Post-dispersal predation of *Vouacapoua* seeds occurs early and only on ungerminated seeds. The lack of interest by rodents in germinated seeds or cotyledons of young seedlings combined with the rapid exhaustion of endosperm reserves (pers. obs.) suggest that germinated seeds offer insufficient rewards to rodents during the long dry season when fruits are scarce (Sabatier 1985).

Large seeds of *Vouacapoua* can only be disseminated by big rodents (*Myoprocta exilis*, *Dasyprocta leporina*, *Agouti paca*, *Sciurus aestuans*, and *Proechimys* spp.) and from the nature of the hoards only acouchies and agoutis seem to be efficient despite the destruction of some dispersed seeds. In the case of *Vouacapoua* the proportion of dispersal attributable to each of the two caviomorph rodents present in French Guiana is not known. Data from Sabatier (1983) and my observations lead me to believe that acouchies are more effective.

In conclusion, scatter-hoarding by caviomorph rodents results in short distance seed dispersal which is very efficient with respect to seed survival. The behaviour of certain Dasyproctidae promotes dispersal of *Vouacapoua* seeds and allows seeds to escape other predators (Janzen 1970). These features evoke a mutualistic system (Herrera 1985) with reciprocal advantages for both the animal and the plant. On the one hand, seeds of *Vouacapoua* are a principal food of rodents. On the other hand, rodents play an active part in the recruitment of the plant: by scatter-hoarding they appear to prevent the destruction of the unburied seeds and to enlarge the recruitment area of the parent tree.

ACKNOWLEDGEMENTS

This paper is part of a thesis for the degree of Doctor of the Université Paris 6. It was supported by a grant from the Ministère de l'Industrie et de la Recherche,

by the ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération), by the Muséum National d'Histoire Naturelle de Paris and by the Ministère de l'Environnement. I am specially grateful to Gérard Dubost who guided my first steps on the way to rodent ecology and for all the discussions we had about acouchies and agoutis, and to Louise Emmons, Nicholas V. L. Brokaw, Nicholas Smythe, the editorial board and two anonymous reviewers for their criticism and suggestions for improving the English text. Gérard Tavakilian (ORSTOM) and Hélène Perrin (MNHN) provided the insect identification.

LITERATURE CITED

- BROKAW, N. V. L. 1982. The definition of treefall and its effects on measures of forest dynamics. *Biotropica* 14:158-160.
- DUBOST, G. 1988. Ecology and social life of the red acouchy, *Myoprocta exilis*; comparisons with the orange-rumped agouti, *Dasyprocta leporina*. *Journal of Zoology of London* 214:107-123.
- GUILLOTIN, M. 1981. Données écologiques sur les petits rongeurs forestiers terrestres de Guyane française. Thèse de 3ème cycle. USTL Montpellier.
- HALLWACHS, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). Pp. 119-135 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr Junk Publishers, The Hague. 392 pp.
- HERRERA, C. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* 44:132-141.
- HUSSON, A. M. 1978. *The mammals of suriname*. E. J. Brill, Leiden, 569 pp.
- JANZEN, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23:1-27.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501-528.
- JANZEN, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6:69-103.
- KILTIE, R. A. 1981. Distribution of palm fruit on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica* 13:141-145.
- McHARGUE, L. A. & HARTSHORN, G. S. 1983. Seed and seedling ecology of *Carapa guianensis*. *Turrialba* 33:399-404.
- MORRIS, D. 1962. The behaviour of the green acouchi (*Myoprocta pratti*) with special reference to scatterhoarding. *Zoological Society of London Proceedings* 139:701-733.
- MURIE, J. O. 1977. Cues used for cache finding by agouti (*Dasyprocta punctata*). *Journal of Mammalogy* 58:95-96.
- ROBERTS, E. H. 1973. Predicting the storage life of seeds. *Seed Science and technology* 1:499-514.
- SABATIER, D. 1983. Fructification et dissémination en forêt guyanaise. Thèse de 3ème cycle. USTL Montpellier.
- SABATIER, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Revue d'Ecologie (Terre et vie)* 40:289-320.
- SMYTHE, N. 1978. The natural history of the central American agouti (*Dasyprocta punctata*). *Smithsonian Contributions to Zoology* 257, 52 pp.
- SORK, V. L. 1985. Germination response in a large-seeded neotropical tree species. *Gustavia superba* (Lecythidaceae). *Biotropica* 17:130-136.

Accepted 6 March 1990