FRUGIVORY AND SEED DISPERSAL BY RED HOWLER MONKEYS : EVOLUTIONARY ASPECT

Catherine JULLIOT*

The study of interactions between fruits and their vertebrate consumers especially in tropical forests has generated a great deal of interest in recent decades. Several studies have shown that morphological characteristics of fruits are involved in fruit choice by frugivores (e.g. Snow, 1971 ; Janson, 1983 ; Gautier-Hion *et al.,* 1985). On the other hand, fruit characteristics may have evolved under consumer pressures as a result of the consumer role as seed dispersers (Snow, 1971 ; McKey, 1975 ; Janzen, 1980 ; Howe & Smallwood, 1982 ; Charles-Dominique, 1993).

In this paper, the main interactions between Red Howler Monkeys (*Alouatta seniculus*) and the plants they use as fruit resources are presented in order to show patterns of seed dispersal by howler monkeys, in the case of a particular Sapotaceae species, *Chrysophyllum lucentifolium.* The results are discussed as regards to « diffuse coevolution » between primates and fruiting plants, especially those of the Sapotaceae family which is the most abundant plant family and that most exploited by howler monkeys at the study site.

MATERIAL AND METHODS

STUDY SITE

The field study was conducted at the Nouragues station (4° 05 N, 52° 40 W) in French Guiana, during a two year period (April 1988 to May 1990) including 19 months of observation of a single howler monkey troop. The habitat consists of tropical rain forest with a continuous canopy 30 to 40 meters high, with some trees growing to 65 meters in height (Sabatier & Prévost, 1990). The study area is totally uninhabited, and has not sustained any human activity for two hundred years.

ANIMAL SPECIES

The Red Howler Monkey is one of the largest primates in South America with a body mass ranging from 6 to 8 kg (Thorington *et al.,* 1979). It is strictly

* CNRS-URA 1183, Laboratoire d'Ecologie Générale, Muséum National d'Histoire Naturelle, 4 av. du Petit Château, F-91800 Brunoy.

vegetarian and probably the most folivorous neotropical primate (e.g. Milton, 1980 ; Crockett & Eisenberg, 1987 ; Julliot & Sabatier, 1993). At the beginning of the study, the focal troop was composed of 6 members including 1 adult male and 2 adult females. The troop was observed during 3-5 consecutive days every 2 weeks, over 19 months between April 1988 and May 1990.

DIET

The diet of the troop was determined by direct observation, using the frequency method (Struhsaker, 1975), and by faecal analysis (Julliot & Sabatier, 1993). Faecal samples were also analysed to identify ripe fruit whose seeds were not damaged by their passage through the monkey digestive tract.

FRUGIVORY

In order to determine the howler's fruit choice, we analysed the monkey's selectivity for fruit species in relation to different morphological characteristics of fruit. These characteristics are described from the monkey's viewpoint. According to a typology used by Sabatier (1983), characters retained are (Table I) :

a) fruit category : we regrouped fruit species presenting the same aspect to animals, taking into account the presence of pulp, presence of a protective coat and dehiscence of the coat. Four fruit categories were so determined ;

b) resistance of the external coat of fruit : five degrees of resistance were determined ;

c) fruit weight, fruit colour and type of pulp. Two classes of pulp were defined according to the water content, and a third class was added for fleshless fruit ;

d) seed number, seed weight and seed protection. Four degrees of protection were determined.

SEEDLING CENSUS

For five plots 40 m × 32 m, each including a monkey's sleeping site, the census of seedlings less than 1 m high was compared with reference plots for 7 plant species consumed by howler monkeys. Plots were divided according to a 2 m × 2 m grid and every second quadrat of 4 m^2 was sampled. Thus, 160 quadrats per plot were sampled. The method of spatial autocorrelation matrix was used to analyse the spatial distribution of seedlings (Chessel, 1981).

In this article, we analyse only the results for *Chrysophyllum lucentifolium* (Sapotaceae), and only consider the three batches whose sleeping site plot and reference plot do not include fruiting tree of this species.

RESULTS

DIET COMPOSITION

The died of the troop was composed of 57 % of leaves, 25 % of fruit and 12 % of flowers. Among the 195 plant species eaten, 90 were eaten as ripe fruits

TABLE I

Morphological characteristics of fruit species used for the analysis of fruit consumed by Red Howler Monkeys

A-FRUITS :

Fruit categories :
- — *Berry* (fruit with external pulp)
- — *Capsule* (fleshy fruit with external dehiscent coat)
- — *Cacao-pod-like* (fleshy fruit with external indehiscent coat)
- — *Pod* (fleshless fruit with external dehiscent coat)

Resistance of external indehiscent coat :
- — Can be crushed between fingers of humans
- — Can be opened easily with fingernail of humans
- — Difficult to open with fingernail of humans
- — Can easily be opened with a knife
- — Difficult to open with a knife

Weight : < 5 gr, 5-50 gr, 50 gr

Colour : yellow, orange, red, purple, green, white, bicoloured*

Type of pulp : juicy, dry, fleshless fruit

B-SEEDS :

Number : 1-2, 3-5, 6-10, 10-50, > 50

Weight : ≤ 0.1 gr, 0.2-0.9 gr, 1-2 gr, 3-4 gr, ≥ 5 gr

Protection :
- — no protection
- — can be opened with fingernail
- — can only be opened with a knife
- — cannot be opened even with a knife

* all bicoloured fruits are white and red (Burseraceae)

(Julliot & Sabatier, 1993). The most important family was the Sapotaceae which represented about 19 % of fruit consumption ; *Chrysophyllum lucentifolium* was the most exploited species.

FRUIT CHARACTERISTICS

The analysis of fruit characteristics showed that howler monkeys mainly consumed small- or medium-sized fruit with yellow, orange or red colour, juicy pulp and few well protected seeds (Table II).

Among the 90 plant species exploited for ripe fruit, 17 species have a very resistant and indehiscent external coat (fourth and fifth degrees of hardness), and 15 of them are of the Sapotaceae.

GERMINATION TESTS

Howler monkeys disperse by endozoochory more than 95 % of the ripe fruit species that they eat. Germination tests have been done for 17 of the most

TABLE II

Main morphological characteristics of fruit species consumed by Red Howler Monkeys

	Proportion of fruit consumption
Fruit : < 5 gr, 5-50 gr	77.4 %
Colour : yellow, orange, red	64.7 %
Type of pulp : juicy	76.5 %
Number of seeds : 1-5	72.0 %
Seeds protection : second to third degree	66.3 %

TABLE III

Comparison of germination rates and germination latency between ingested seeds and fresh seeds, for respectively 17 and 15 plant species exploited by the Red Howler Monkey troop

	Number of species
Germination rate	
(according to the binomial law for p = 0.05)	
ingested seeds > fresh seeds	3
ingested seeds < fresh seeds	7
similar germination rates	7
Germination latency	
(significant difference for p < 0.05)	
ingested seeds > fresh seeds	2
ingested seeds < fresh seeds	1
similar germination rates	12

consumed species including two Sapotaceae species (Julliot, in press). Results revealed that the action of the digestive tract of howler monkeys does not modify the germinative power of most ingested seeds (Table III).

PATTERNS OF SEED DISPERSAL : EXAMPLE OF *CHRYSOPHYLLUM LUCENTIFOLIUM* (SAPOTACEAE)

The comparison between location of fruiting trees exploited by the monkey troop and howler's defecations containing seeds of the same species showed that monkeys can disperse seeds far from parental trees. The distance of seed dispersal has been measured for 17 plant species, including 8 Sapotaceae : dispersal can reach 550 meters, with a mean of 260 meters (± 129 m, n = 76). The distance of seed dispersal for *Chrysophyllum lucentifolium* varies from 0 m to 400 m (Fig. 1).

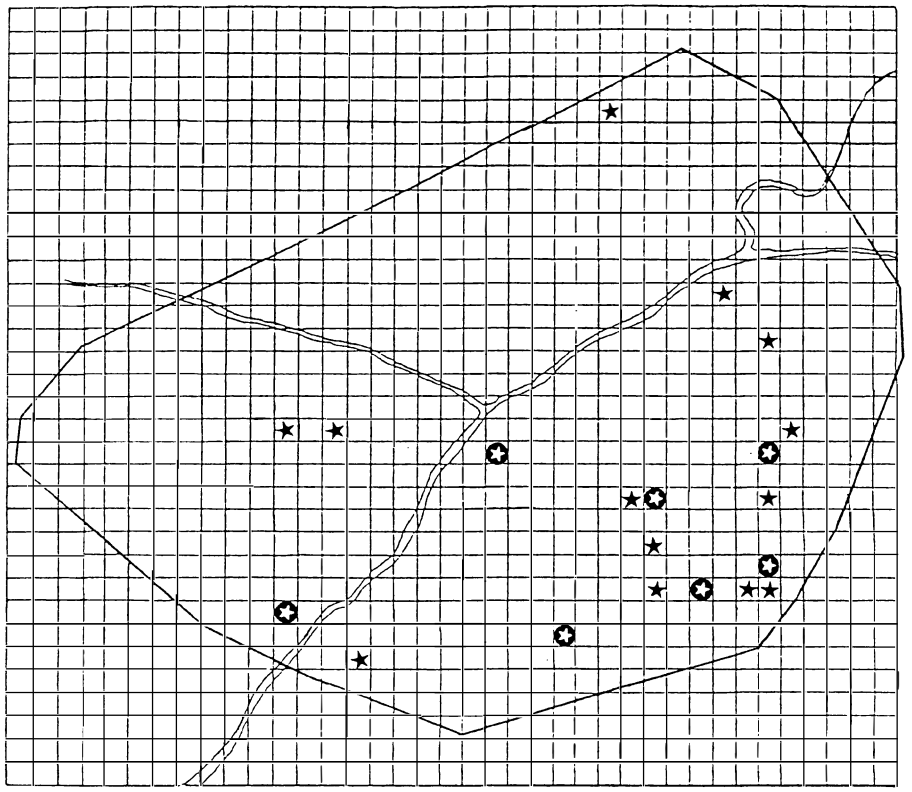

Figure 1. — Localization of *Chrysophyllum lucentifolium* (Sapotaceae) fruiting trees exploited by the monkey troop and defecations containing seeds of *Chrysophyllum lucentifolium*, based upon a 25 m × 25 m grid-map of the troop home range.

Moreover, certain aspects of the behaviour of howlers promote a particular pattern of seed dispersal. These monkeys regularly use a limited number of sleeping sites and exhibit a very long digestive time (20 h 40 ± 3 h 03, n = 6 ; Julliot, 1992). Consequently, we observed a concentration of defecations (60 %, n = 250) under the sleeping sites (Fig. 2).

SEEDLING CENSUS OF *CHRYSOPHYLLUM LUCENTIFOLIUM* (SAPOTACEAE)

The census of *Chrysophyllum lucentifolium* seedlings (Table 4) showed a significant difference favouring of sleeping site plots (G-test : G = 18.108, df = 2, $p < 0.001$). We also noted a particular spatial distribution of seedlings on the two

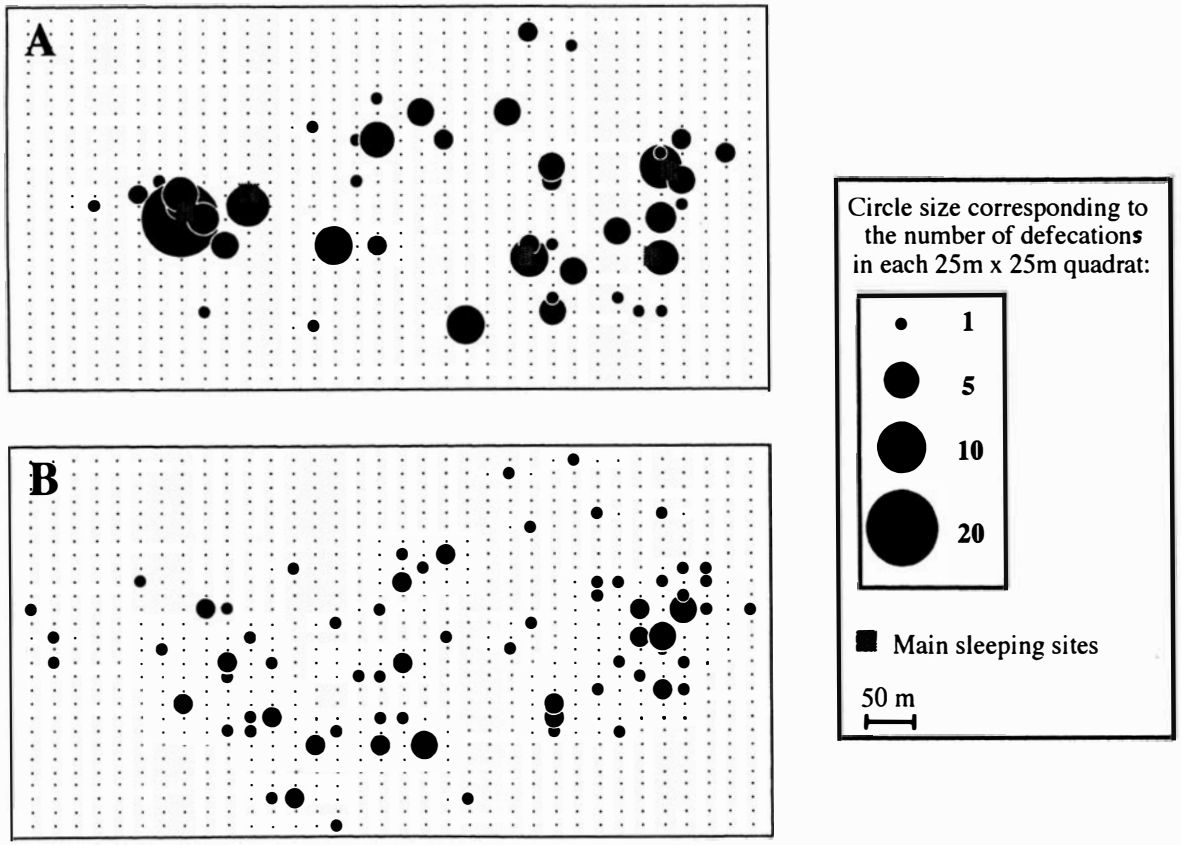

Figure 2. — Spatial distribution of defecations under the sleeping sites (A) and in other places (B).

sleeping site plots where they are sufficiently numerous (Fig. 3). The spatial autocorrelation matrix indicates that seedlings have an aggregative distribution on these two sleeping site plots (Geary's index significant for small size of blocks), although the spatial distribution of seedlings is not structured on the reference plots. Moreover, the seedling aggregates are located at the main points of monkey defecation around the sleeping tree. For this species of Sapotaceae results clearly indicate that seed dispersal by howler monkeys is favourable to seed germination and seedlings' development.

TABLE IV

Comparison of seedling census of Chrysophyllum lucentifolium *(Sapotaceae) on three plots including a Red Howler Monkey sleeping site and reference plots*

	Number of seedlings	
	sleeping site plot	reference plot
batch 1	89	0
batch 2	10	2
batch 3	82	12
Total	181	14

DISCUSSION

The characteristics of fruit exploited by Red Howler Monkeys at our study site are in accordance with the primate syndrome defined by Gautier *et al.* (1985) for African primates. However, two other characteristics are determinant for seed dispersal by limiting the number of potential dispersers.

Except for some parrots which are seed predators, only mammals can open hard and indehiscent external coats. Our results have shown that howler monkeys can open fruit with a very hard indehiscent external coat. Moreover, our observations have shown that these monkeys can ingest seeds 4 cm long and 2 cm large without damaging them (Julliot, in press). Only the Spider Monkey (*Ateles paniscus*), a sympatric primate of similar size, is known to ingest such large seeds (Roosmalen, 1985).

Thus, howler monkeys, and probably other primates such as spider monkeys, can be associated with the seed dispersal of plants whose fruits have hard and indehiscent external coat and/or large seeds that most birds and small mammals cannot ingest. This is the case of the Sapotaceae whose fruit often simultaneously showed both characteristics and was, moreover, the dominant plant family in the monkey's diet, at the Nouragues station. During the field study, the focal monkey troop dispersed at least 50 % of the Sapotaceae species recorded on their home range (Sabatier & Prévost, 1990). So, it appears that the most exploited plant family by howler monkeys also mainly depends on them for the seed dispersal.

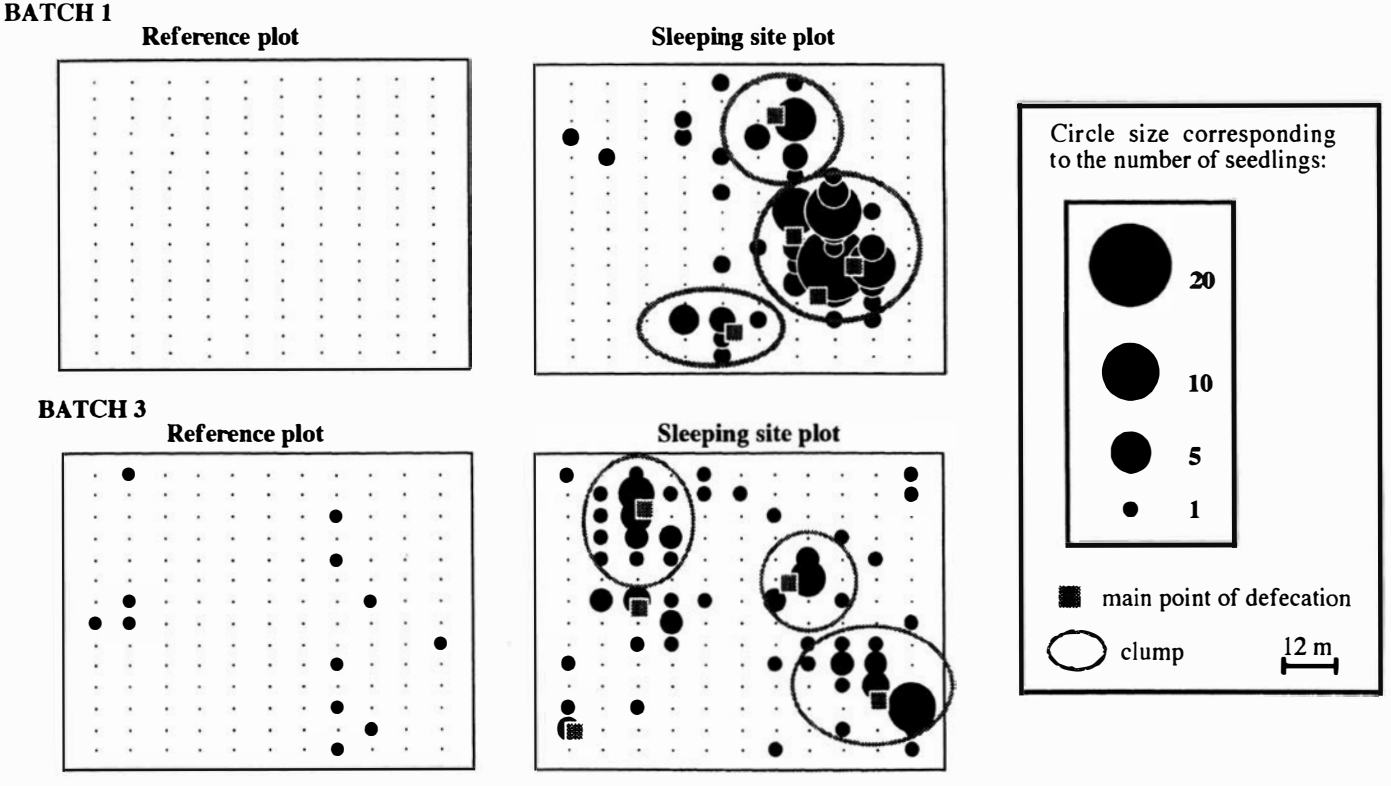

Figure 3. — Distribution of seedlings of *Chrysophyllum lucentifolium* (Sapotaceae) on two plots including a sleeping site of the monkeys compared with two reference plots.

For Sapotaceae species, seed dispersal by Red Howler Monkeys can be characterised by the following points : maintenance of the germinative power of ingested seeds, distribution of seeds away from the parental tree in accordance with the « Escape Hypothesis » (Janzen, 1970 ; Connell, 1971), and important seedling development under main sites of seed dispersal in accordance with the « Direct Dispersal Hypothesis » (Howe & Smallwood, 1982). Thus, howler monkeys may be considered as efficient dispersers of Sapotaceae. Moreover, the aggregative pattern of seed dispersal by howler monkeys could be at the origin of the clumped distribution of most Sapotaceae species, a characteristic shared with many tropical plant species.

It not only appears that howler monkeys are efficient dispersers of Sapotaceae species, but also that fruits of Sapotaceae display characters that can be considered as evolutionary responses to the selective pressure of Primates, which are their main consumers and dispersers. These feature are :

1) the indehiscent and hard external coat that most birds and small mammals cannot open,

2) the coloration of fruits when they are ripe : usually, yellow or orange, which are the colours preferentially chosen by Neotropical primates, as well as Afrotropical primates, according to other studies (e.g. Janson, 1983 ; Gautier-Hion *et al.,* 1985) ; and,

3) Sapotaceae often bear large fruit with few large seeds that only large mammals are able to ingest.

It is probable that the relationship between primates and Sapotaceae for seed dispersal exists in other tropical forest where these two families are present together. In this case, the relationship between primates and Sapotaceae may correspond to the « diffuse coevolution » proposed by Janzen (1980), which considered the selective pressures exerted between one group of animal species and one group of plant species linked by mutualistic interactions.

Because of the large difference of generation time between mammals and plants, it is unlikely that actual primates, and in particular howler monkeys, are involved at the origin of the development of such fruit characteristics of Sapotaceae species. But, it is now admitted that hereditary phenotypic characteristics of plants and their actual dispersers have not necessarily evolved together. A recent theory of coevolution proposed by Charles-Dominique (1993) considers that « the global situation of an ecosystem will represent a juxtaposition of numerous old coevolutionary systems, from which many of them are in a stable phase maintained by animal partners that have not necessarily contributed to their original evolution ». The relationship between primates and Sapotaceae may correspond to this theoretical scheme, present primates taking the place of extinct dispersers.

It will be interesting to analyse the relationships between other primates and the family Sapotaceae at the Nouragues station, where this plant family is very abundant, and also to verify if such relations effectively exist in other tropical forests.

SUMMARY

The analysis of morphological characters of fruits eaten by Red Howler Monkeys (*Alouatta seniculus*) in French Guiana, shows that howlers mainly

consumed juicy fruits with bright colours and few well protected seeds. However, monkeys can be associated with seed dispersal of species bearing fruit with a hard and indehiscent external coat, that only mammals are able to open with their teeth, or with large seeds that most birds, bats, or other small frugivorous animals cannot ingest. This happens in the family Sapotaceae the fruits of which often simultaneously show both characteristics, and which is the dominant family in this monkey's diet, at the Nouragues Station. We also observed that the howler monkey and probably other frugivorous primates like the Spider Monkey (*Ateles paniscus*), is one of the main consumers and dispersers of Sapotaceae in our study site. An analysis of seedling populations under sleeping sites of howler monkeys indicates that they could be considered as efficient dispersers for this plant family. Moreover, the aggregative pattern of seed dispersal by howlers could be at the origin of the clumped distribution of most Sapotaceae. All these observations enable us to hypothesise the occurrence of a « diffuse coevolution » between primates and fruits of the Sapotaceae.

RÉSUMÉ

L'analyse des caractéristiques morphologiques des fruits consommés par les singes hurleurs roux (*Alouatta seniculus*), en Guyane française, montre que les hurleurs choisissent préférentiellement des fruits pulpeux, de coloration vive et comprenant un petit nombre de graines bien protégées. Cependant, les primates peuvent être associés à la dissémination d'espèces dont les fruits ont soit une enveloppe externe indurée et indéhiscente que seuls les mammifères peuvent ouvrir à l'aide de leurs dents, soit des graines de grande taille que les oiseaux, les chauves-souris ou les autres petits animaux frugivores ne peuvent ingérer. Les fruits de Sapotaceae présentent simultanément les deux caractéristiques ; cette famille est, de plus, dominante dans le régime alimentaire des hurleurs à la Station des Nouragues. Nous avons également observé que le singe hurleur est, probablement avec les autres primates frugivores comme le singe araignée (*Ateles paniscus*), l'un des principaux consommateurs et disséminateurs des Sapotaceae sur le site d'étude. L'analyse du peuplement de plantules sous les dortoirs des singes hurleurs a montré qu'ils étaient des disséminateurs efficaces, en particulier pour cette famille végétale. Par ailleurs, les singes hurleurs ont un mode agrégatif de dissémination des graines qui pourrait être à l'origine de la répartition par taches de la plupart des Sapotaceae. Toutes ces observations permettent d'envisager l'existence d'une « coévolution diffuse » entre les primates et les fruits de Sapotaceae.

ACKNOWLEDGEMENTS

This study was supported by CNRS (URA 1183). I would like to thank Dr. D. Sabatier (botanist, ORSTOM) for identifying all the plant species collected for this study.

REFERENCES

CHARLES-DOMINIQUE, P. (1993). — Speciation and coevolution : an interpretation of frugivory phenomena. *In :* Fleming, T.H. and Estrada, A. (eds.), *Frugivory and Seed Dispersal : Ecological and Evolutionary Aspects,* pp. 75-84. *Vegetatio,* 107/108. Kluwer Acad. Publishers.

CONNELL, J.H. (1971). — On the role of natural ennemies in preventing competitive exclusion in some marine animals and rain forest trees. *In :* Den Boer P.J. & Gradwell G.R. (eds.), *Dynamics of populations,* pp. 298-312. Washington : PUDOC.

CROCKETT, C.M. & EISENBERG, J.F. (1987). — Howlers : Variations in group size and demography. *In :* Smuts, B.B., Cheyney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T. (eds.), *Primate societies,* pp. 54-68. Univ. Chicago Press, Chicago-London.

GAUTIER-HION, A., DUPLANTIER, J.-M., QURIS, R., FEER, F., SOURD, C., DECOUX, J.-P., DUBOST, G., EMMONS, L., ERARD, C., HECHESTWEILER, P., MOUNGAZI, A., ROUSSILHON, C. & THIOLLAY, J.M. (1985). — Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia,* 65 : 324-337.

HOWE, H.F. (1980). — Monkey dispersal and waste of a neotropical fruit. *Ecology,* 61 : 944-959.

HOWE, H.F. & SMALLWOOD, J. (1982). — Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.,* 13 : 201-228.

JANSON, C.H. (1983). — Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science,* 219 : 187-189.

JANZEN, D.H. (1970). — Herbivores and the number of tree species in tropical forest. *Am. Nat.,* 104 : 501-528.

JANZEN, D.H. (1980). — When it is coevolution ? *Evolution,* 34 : 611-612.

JULLIOT, C. (1992). — *Utilisation des ressources alimentaires par le singe hurleur roux,* Alouatta seniculus *(Atelidae, Primates), en Guyane : impact de la dissémination des graines sur la régénération forestière.* Thèse de Doctorat, Université de Tours.

JULLIOT, C. (in press). — Seed dispersal by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest, at the Nouragues station in French Guiana. *Biotropica.*

JULLIOT, C. & SABATIER, D. (1993). — Diet of the Red Howler Monkey (*Alouatta seniculus*) in French Guiana. *Int. J. Primatol.,* 14 : 527-550.

MCKEY, D. (1975). — The ecology of coevolved seed dispersal systems. *In :* Gilbert, L.E. & Raven, P.H. (eds.), *Coevolution of animals and plants,* pp. 159-191. Univ. of Texas Press, Austin, Lond.

MILTON, K. (1980). — *The foraging strategy of howler monkeys. A study in primate economics.* Columbia Univ. Press, New York.

ROSSMALEN, M.G.M. (1985). — Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazonica,* 19 : 238 pp.

SABATIER, D. (1983). — *Fructification et dissémination en forêt guyanaise. L'exemple de quelques espèces ligneuses.* Thèse de 3e cycle, Univ. des Sciences et Techniques du Languedoc, Montpellier.

SABATIER, D. & PREVOST, M.F. (1990). — Variations du peuplement forestier à l'échelle stationnelle : le cas de la station des Nouragues en Guyane française. *Actes de l'Atelier sur l'Aménagement et la Conservation de l'Ecosystème forestier tropical humide,* 12-16 mars 1990, pp. 169-187. MAB-UNESCO.

SNOW, D.W. (1971). — Evolutionary aspects of fruit-eating by birds. *Ibis,* 113 : 194-202.

STRUHSAKER, T.T. (1975). — *Five new world primates.* Princeton : Princeton University Press.

THORINGTON, R.W. Jr., RUDRAN, R. & MACK, D. (1979). — Sexual dimorphism of *Alouatta seniculus* and observations on capture techniques. *In :* Eisenberg, J.F. (ed.), *Vertebrate ecology in northern Neotropic,* pp. 97-106. Washington D.C. : Smithsonian Inst. Press.