FRUIT CHARACTERS IN THE DIET
OF SYNTOPIC LARGE FRUGIVOROUS FOREST BIRD SPECIES
IN FRENCH GUIANA

Christian Erard[1], Marc Théry[1] & Daniel Sabatier[2]

Résumé. — *Les caractères des fruits consommés par les grands oiseaux frugivores syntopiques en forêt guyanaise française*. — Les caractéristiques des plantes sur lesquelles les quatre grandes espèces frugivores aviennes de Guyane française (*Tinamus major*, Tinamidae ; *Psophia crepitans*, Psophiidae ; *Crax alector* et *Penelope marail*, Cracidae) basent leur régime alimentaire ont été analysées. Les caractéristiques de 102 espèces végétales et de leurs fruits ont été comparées afin de détecter d'éventuels syndromes propres à chaque espèce avienne. Des analyses multifactorielles ont été conduites tant à partir du nombre d'espèces végétales que de la quantité de fruits de chaque espèce végétale consommée par chaque espèce avienne. Certains caractères des fruits sont associés à une espèce d'oiseau particulière et plus particulièrement selon qu'il s'agit d'un disséminateur ou d'un destructeur des graines. Une possible distinction transparaît entre les consommateurs selon qu'ils sont arboricoles ou terrestres. Ces associations entre frugivores et traits des fruits et des plantes qui les produisent sont discutées en termes de valeur pour la dissémination des plantes et de probabilité d'attraction de disperseurs par opposition à la défense contre les prédateurs de graines. Les interactions entre les plantes et les consommateurs relèvent du mutualisme (bénéfices tant pour la plante que pour l'oiseau) dans le cas de *Penelope* et de *Psophia* mais pas dans celui de *Crax* et de *Tinamus*, bien que *Crax* puisse disséminer certaines plantes dont les graines, très petites, transitent sans altération dans son tube digestif. Cette étude souligne une fois encore le besoin d'études plus larges à l'échelle des peuplements des interaction plantes-animaux.

Summary. — Characteristics of the plants on which the four largest arboreal and terrestrial forest frugivorous bird species of French Guiana (*Tinamus major*, Tinamidae; *Psophia crepitans*, Psophiidae; *Crax alector* and *Penelope marail*, Cracidae) base their diet were compared. The characteristics of 102 plant species and their fruits were compared in order to determine whether some syndromes were associated with particular bird species. Multifactorial analyses were conducted using either number of plant species or quantity of fruits of each plant species ingested by each bird species. Sets of fruit character-states are associated with particular bird species such that distinct traits are linked to seed-predation or seed-dispersal. A possible separation between arboreal and terrestrial consumption is also indicated. These associations between avian frugivores and fruit and fruiting plants' traits are discussed in terms of their dispersal value to plant species and the likelihood of attracting seed-dispersers as opposed to defending seeds against predators. The interactions between fruiting plants and consumers are considered mutualistic (benefit both the plant and the bird) in the case of *Penelope* and *Psophia*, but are predator-prey interactions in that of *Crax* and *Tinamus*, although *Crax* may be a disperser for some plants whose small seeds pass unaltered through its digestive tract. The study highlights once more the need for more community-wide approaches to plant-animal interactions.

Frugivory plays an important role in the structuring of tropical rain forest bird communities (e.g. Terborgh, 1980; Beehler, 1981; Brosset & Erard, 1986; Erard, 1986, 1989; Karr, 1989; Brosset, 1990; Robinson *et al.,* 1990; Charles-Dominique, 2001; Thiollay *et al*., 2001; Chen

---

[1] CNRS / Muséum National d'Histoire Naturelle UMR 7179, Département d'Ecologie et de Gestion de la Biodiversité, 4 avenue du Petit Château, F-91800 Brunoy. E-mail: erard@mnhn.fr & thery@mnhn.fr

[2] IRD, UMR AMAP, TA A-51 PS2. F-34398 Montpellier Cedex 5, France. E-mail: dsabatie@mpl.ird.fr

et al., 2004); thus in French Guiana about 25% of bird species eat fruit (Tostain *et al.,* 1992; Erard & Théry, 1994, 2001). Conversely 70% to 95% of plant species in tropical forests are dispersed by animals, mainly but not only by birds and mammals (e.g. Frankie *et al.,* 1974; Hilty, 1980; Gentry, 1982; Gautier-Hion *et al.,* 1985; Stiles, 1985; Levey *et al.,* 1994; Poulsen *et al.,* 2002; Lord *et al.,* 2002). In French Guiana percentages of plant species dispersed by animals are respectively 72% in secondary successions, 84% in primary forest and 93% for pioneers (Charles-Dominique *et al.,* 1981; Prévost, 1983; Sabatier, 1983, 1985). Consequently, like other frugivores, frugivorous birds are important for the forest dynamics and the evolution of biodiversity (e.g. Robinson & Handel, 1993; Curran & Webb, 2000; Wenny, 2000; Levey *et al.*, 2002; Forget *et al.,* 2002). It is therefore not surprising that during the last decades a quite abundant and still growing literature has been devoted to the analysis of ecological and evolutionary consequences of plant-frugivore interactions (see reviews by Howe, 1986; Willson, 1986; Fleming *et al.,* 1987; Howe & Westley, 1988; Fleming, 1991; Jordano, 1992; Fleming & Estrada, 1993; Cipollini, 2000; Levey *et al.,* 2002, Forget *et al.,* 2002; Herrera & Pellmyr, 2002). Important advances have been made in the characterization of food preferences and/ or choices of consumers and on their role as seed-predators or dispersers. Debates still persist about the coevolutionary aspects of these interactions, particularly because their very nature and level as well as the underlying mechanisms remain far from well understood (see e.g. Howe, 1984; Herrera, 1985, 1986, 2002; Jordano, 1987, 1995; Wheelwright, 1988; Erard & Théry, 1994; Cipollini, 2000; Levey *et al*., 2002).

A number of studies have analysed relationships between fruit characteristics and consumer choices (see e.g. reviews by Estrada & Fleming, 1986; Howe, 1986; Jordano, 1992, 1995; Fleming & Estrada, 1993; Fuentes, 1994; Cipollini & Levey, 1997; Cipollini, 2000). Results showed that birds discriminate between fruits on the basis of a number of features contributing to the attractiveness of the fruit (colour, fruit and/or seed size, shape, fruit type and structure, pulpiness, aspect or state of the fruit, etc.) and to the reward gained by the consumer (e.g. relative ratio of pulp to seed, percent yield of proteins, lipids, sugars and other substances including toxic secondary compounds). The intricacies of the digestive characteristics of the frugivores are now better understood as well as foraging behaviour and morphological characteristics of the consumer in relation to fruiting, dispersal and attractive characteristics of the plants. The frugivore's fruit choice is multifactorial and depends on specific morpho-anatomical, physiological and behavioural traits of the frugivore as modified by environmental and context-sensitive effects with important spatial and temporal variations. To overcome these variations, hierarchical processes of fruit selection may have developed as suggested by Sallabanks (1993).

Although many studies deal with the interactions between plants and a particular species or group of animal species, none fully consider how all animal and plant communities interact at a single place. Nevertheless, some studies (e.g. Gautier-Hion *et al.,* 1985; see also Kitamura *et al*., 2002; Poulsen *et al*., 2002) have made interesting attempts in this direction and have shown how morphological characters of fruits are involved in the choice and partitioning of the available fruit spectrum among consumers (i.e. large canopy birds, rodents, ruminants, elephants and monkeys) and have revealed broad character syndromes of fruit traits associated with different consumer taxa (for such syndromes see also van der Pijl, 1982; Janson, 1983; de Foresta *et al.,* 1984; Dowsett-Lemaire, 1988; Debussche & Isenmann, 1989; Willson *et al.,* 1989; Herrera, 1992a,b; but see Jordano, 1995). Though not necessarily implying coevolution, these dispersal syndromes are important cues for understanding both the organization of trophic niches in the animal community and the coadaptive relations between plants and animals in the system.

In French Guiana's tropical rain forests we focused research on plant-animal interactions, in order to understand and define the role birds play in the dynamics and evolution of these complex ecosystems. We paid particular attention to the four largest arboreal and terrestrial species which are also interesting to study because their biology is still scantily known, and their coexistence and conservation as game species pose ecological problems (Delacour & Amadon, 2004). Previous studies (Erard & Sabatier, 1989; Erard *et al.,* 1991; Théry *et al.,*

1992; Erard & Théry 1994) showed that these large birds are obligate frugivores or seed-eaters, and although there is some overlap in their diet, they have different fruit preferences and, where there is overlap, specific fruits are eaten in different proportions.

In the present paper we want to go further and explore how these large bird species separate into multidimensional fruit-character spaces. We contrast the characteristics of the plants and their fruits with their consumers and examine whether some kind of syndrome can be detected and defined according to the bird species. The aim is to help answer three questions:

(1) Does each of these syntopic and similar-sized species (one is, however, heavier than the other three) choose fruits possessing particular characteristics?

(2) Previous studies have shown that some species eat only the pulp of the fruit (they spit out or defecate the seeds) whereas others eat both pulp and seeds. Do the characteristics of the fruits eaten by each bird species reflect mutualism (i.e. benefits for both the plant and the consumer) or merely predator-prey interaction (i.e. benefits for the consumer but not for the plant which must increase its defense)?

(3) If fruit syndromes can be defined, what can we infer about the role each bird species plays in forest dynamics and of the effects of fruiting variability on the populations of these frugivores?

MATERIALS AND METHODS

STUDY AREA

Data were collected around Saut Pararé, along the Arataye river, a tributary of the main Approuague river (4°02'N, 52°42'W). This site is described in Sabatier (1983) and Maury-Lechon & Poncy (1986) as a lowland rain forest representative of the interior of French Guiana. The area has been uninhabited for several decades and is little hunted (at least before and during the study). At the time of the study, the fauna was complete, i.e. all large animal species were present with most of them being quite regularly observed.

Mean annual rainfall is above 3 m, dividing the year into a long dry season (August to November) and a long rainy season (December to July) with an occasional short dry season in February-March. As shown by studies conducted in adjacent areas, fruiting seasonality is particularly marked among species bearing fleshy fruits dispersed by animals (Sabatier, 1985; Julliot, 1992; Zang, 1994; Larue *et al.*, 2002).

BIRD SPECIES STUDIED

Four species were studied: Great Tinamou *Tinamus major* (Tinamidae), Common Trumpeter *Psophia crepitans* (Psophiidae), Crested Curassow *Crax alector* (Cracidae) and Marail Guan *Penelope marail* (Cracidae). For the sake of convenience they will subsequently be called *Tinamus*, *Psophia*, *Crax*, and *Penelope*.

They are terrestrial except the latter, which is arboreal. Though differently shaped, *Tinamus*, *Psophia* and *Penelope* have similar weights (about 1 kg); *Crax* is larger with a mean weight of 3 kg. Fruits represent the bulk of the diet of these species (Table I), however *Psophia* eats invertebrates as well (for more details see Erard & Sabatier, 1989; Erard *et al.,* 1991 and Théry *et al.,* 1992). According to our present knowledge, *Penelope* and *Psophia* are clearly dispersers that disseminate intact seeds. In contrast, *Tinamus* and *Crax* are predators that destroy the seeds they ingest. However this categorization is rather crude because birds can disperse "intact" seeds that will never germinate because ingestion has altered their germination capacities or simply because they are disseminated to inappropriate sites where they rot or mould, or are destroyed by bacteria, fungi, insects or another seed-predator. On the other hand, seed-predators may ingest small seeds that pass unaltered through their gizzards and germinate.

Though a mobile species in the forest canopy, *Penelope* often stays in the vicinity of clumps of fruiting trees whereas *Psophia* travels more widely through the forest, particularly the moistest parts. In French Guiana, *Psophia* is not particularly dependent on ripe fruits knocked to the ground by monkey troops contrary to what Sherman (1991, 1996) found for *Psophia leucoptera* in Peru. Both *Penelope* and *Psophia* swallow entire fruits or fruit parts and defecate their seeds which retain their germination potential: the large size of the birds (i.e. wide bill-gape) enables them to ingest all the fruits they feed on and not regurgitate the seeds. *Tinamus* appears to be a tramp-predator picking up fruits here and there on the forest floor whereas *Crax* is essentially a mast-eater that remains in limited areas – usually a small forest gap or any place with dense low vegetation where it can reach particular fruiting trees. Both *Tinamus* and *Crax* usually ingest fruits or fruit parts on the forest floor. However, field observations have shown that *Tinamus* may occasionally feed on seeds dropped under roosts of frugivorous bats (i.e. *Artibeus jamaicensis* under palm fronds) and *Crax* may sometimes pick up seeds dispersed on leks by Cocks-of-the rock *Rupicola rupicola* (pers. obs., Théry & Larpin, 1993). Although we never found intact small seeds in intestines or faeces of *Tinamus*, we have shown that in the case of *Crax,* at least some seeds of e.g. *Coussapoa latifolia* pass through its digestive tract intact and germinate (see also Yumoto, 1999, for data on Salvin's Curassow *Mitu salvini*).

Between 1977 and 1985 a sample of digestive tracts of game birds, covering all seasons, was obtained from local people hunting in a 5 km^2 area on the opposite side of the river, in the same forest and more than 5 km downstream from the camp (where CE and DS made detailed ornithological and botanical observations): 17 complete digestive tracts of *Tinamus*, 43 of *Penelope,* 69 of *Crax* and 76 of *Psophia* were thus preserved for later analyses of diets (for details see Erard & Sabatier, 1989; Erard *et al.,* 1991; Théry *et al.,* 1992). These digestive tracts constitute a sample in which all bird species were always represented in the sub-samples so that sample biases (e.g. species A and B represented at time t_1 but only A at time t_2) were much reduced.

In the present paper, our aim is to see whether particular fruit-type(s) correspond(s) to a particular bird species or not. The question was not whether our fruit sample included a large proportion of fruit species consumed by each bird species but instead whether it represented accurately the fruit-types searched for by every bird species. Because our sample covers several years and seasons and is based on significant series of digestive tracts (except perhaps for *Tinamus*), we assumed that accurate definitions of fruit-types can be derived from it for each bird species.

PLANT SPECIES STUDIED

The four studied bird species consume fruits of at least 141 plant species in French Guiana (*Penelope*: 24, *Tinamus*: 38, *Psophia*: 55, *Crax*: 80; see Erard *et al.,* 1991; Théry *et al.,* 1992). Plant identifications were based on comparisons of fruits and seeds found in the digestive tractus with a reference field collection and botanical vouchers deposited at the Cayenne Herbarium (CAY). Thirty six species of seeds were unidentified and were not considered further. We also excluded from the analyses the three dry pulpless fruit species picked up by *Crax* (1 species) and *Psophia* (2 species): their small size and extreme hardness suggest they were taken into the digestive tract as grit rather than food. The remaining 102 plant species are representative of the diet of each bird species (Tab. I, Appendices 1, 2 and 3).

TABLE I

Importance of the 102 fruit species in the whole diet and in the fruit part of the diet of the studied frugivores

Bird species	% whole diet	% fruit part	Number of fruit species	Total fruit
Crax alector	88.6	97.2	59	91.2
Penelope marail	91.6	94.1	20	97.4
Psophia crepitans	78.0	93.8	43	83.2
Tinamus major	88.3	99.3	35	89.0

% whole diet: quantity of ingested fruits of the 102 plant species as a percentage of the whole diet (fruits + other plant or non plant food).% fruit part: quantity of ingested fruits of the 102 plant species as a percentage of the fruit part of the diet; total fruit: total percentage of fruits in the species' diet.

Based on D. Sabatier's knowledge of the fruiting trees in French Guiana, each fruit species was described using nine variables: (1) growth form, (2) fruit and (3) flesh type, (4) fruit colour, (5) fruit and (6) seed mechanical protection, (7) number of seeds, (8) fruit availability and (9) species abundance (column S of Appendix 2 summarizes the distribution of each variable in the entire fruit sample). Variables were then subdivided into 40 character-states:

1. Growth form: (a) shrub (or sapling) or low-climbing liana (< 2 m); (b) small tree (2-10 m); (c) middle understory tree (10-20 m); (d) epiphyte; (e) liana reaching the canopy; (f) tall tree (canopy and emergent trees).
2. Fruit type: (a) berry-like; (b) drupe-like; (c) dehiscing capsule; (d) pod-like (non dehiscing capsule) (see Erard *et al.*1989); hereafter respectively referred to as berry, drupe, capsule and pod *sensu lato*.
3. Consistency of edible tissue (decreasing water content and increasing fibre content): (a) very soft and juicy; (b) fleshy thin; (c) fleshy thick.
4. Colour (external colour of ingested item): (a) black and dark purple; (b) yellow; (c) brown; (d) red; (e) blue; (f) green; (g) white. For multicoloured fruits only the colour of the external surface of the edible portion was considered.
5. Fruit protection (at the stage of consumption): resistance presented by the outer coat preventing access to flesh and seed. (a) no protection: f1; (b) easy to open: f2; (c) difficult to open with fingernails: f3; (d) can only be opened with a knife: f4.
6. Seed protection: (a) no protection: s1; (b) easy to burst: s2; (c) difficult to burst with fingernails: s3; (d) can only be parted with a knife: s4; (e) cannot be cut with a knife: s5.
7. Number of seeds per fruit: (a) 1-2; (b) 3-10; (c) 11-100; (d) >100.
8. Available fruit production (individual crop size). (a) < 10; (b) 10-100; (c) > 100-< 1000; (d) > 1000 ripe fruits.
9. Species abundance: (a) rare; (b) frequent (scattered, not abundant); (c) abundant.

DATA PROCESSING

Data used in the present study are both qualitative (see fruit variables and character-states above) and quantitative (relative importance of each fruit species in the diet of each bird species; frequency and percentage distribution of the plant species according to their biological, abundance and fruit characteristics in the diet of each bird species, see appendices 1, 2 and 3).

As in Gautier-Hion *et al.* (1985), to test for association between fruit characters, we used a symmetrical contingency table of dimensions 40 x 40 with the 40 character-states of the 9 variables mentioned above, where F (i, j) is the number of times a fruit with character-state i also has character-state j. Likewise, correlation between fruit characters and bird species was examined on a 40 x 4 contingency table were C (i, j) is the frequency of fruits with character-state i in the diet of bird species j. Each fruit character can be examined in a 4 dimensional frugivore space and each frugivore seen in a 40 dimensional fruit-character space. Two 40 x 4 contingency tables were constructed. One expressed frequencies in number of fruit species with character-state i eaten by bird species j. The other expressed frequencies in quantities (wet weight) of fruit species with character-state i ingested by bird species j.

These three contingency tables were investigated by principal component analysis of correlation matrices. This method, which does not require that tables be non-singular (Johnson & Wichern, 1992), seeks to account for most of the total system variability using a low number of variables called principal components. Best discrimination plots are obtained when variables are well distributed around a correlation circle. Two graphical representations were drawn using the ADE software (CNRS UMR 5558) by superimposing the projections of points and vectors in the space as biplots of Gabriel (1971), also named covariance biplots by Ter Braak (1983).

Three principal components analyses were run. The first one was conducted on the contingency table of dimensions 40x40 in order to illustrate associations between fruit characters without consideration of how much and by which particular bird species they were consumed. It is merely aimed at displaying how the various fruit and plant character-states are linked among the 102 plant species we considered. Contrasted with those resulting from two other analyses (based on the distribution of these plant species among the four consumers), pattern(s) detected by this analysis will help to define fruit-syndromes associated with each consumer. The second and third analyses were based on contingency tables of dimension 40x4 with frequencies expressed either as numbers of fruit species, or quantities of fruit ingested. They were conducted in order to explore a possible difference between potential (2nd analysis) and effective (3rd analysis) choices of fruit made by these frugivores. Indeed, compared to those of 2nd analysis, results from 3rd analysis could be more constrained by intra- and interspecific competition and environmental effects. The second analysis was aimed at testing for qualitative fruit selection by the four bird species, i.e. do the four bird species eat fruits displaying the same fruit and plant character-states? The third analysis was intended to go deeper into fruit selection by taking into account not only whether the fruit is eaten, but also how much is eaten. This 3rd analysis is expected to reflect fruit preferences but may be more sensitive to local conditions than the second. Because ingested quantities, not merely number of fruit species, are taken into consideration, the 3rd analysis will be less representative of the kind of fruits each bird species ingests than of the fruit characters these birds use to share local fruit resources. Patterns resulting from the 3rd analysis integrate more local conditions of fruit availability and interactions between bird species than those resulting from the 2nd analysis.

RESULTS

ASSOCIATION BETWEEN FRUIT VARIABLES AND BETWEEN FRUIT CHARACTER-STATES

Because of a most likely phylogenetic effect we would have expected a lot of correlations between fruit variables but only five significant ones were detected (Table II): (i) between growth form and fruit availability ($P < 0.001$), (ii) between fruit type and number of seeds ($P < 0.001$), (iii) between number of seeds and fruit protection ($P < 0.01$), (iv) between fruit production and seed protection ($P < 0.01$), and (v) between fruit colour and flesh type ($P < 0.05$). These variables are important for the consumers.

TABLE II

Pearson correlation coefficients between the nine fruit variables

	Growth form	Fruit type	Flesh type	Fruit colour	Fruit protection	Seed	Number seeds	Fruit availability
Fruit type	- 0.050							
Flesh type	0.112	- 0.017						
Fruit colour	0.049	0.126	0.218*					
Fruit protection	0.029	0.087	0.054	0.097				
Seed protection	0.153	- 0.126	0.184	0.061	0.039			
Number of seeds	0.073	0.398***	0.104	0.013	0.313**	0.020		
Fruit availability	0.507***	0.145	0.113	- 0.104	- 0.065	0.284**	0.097	
Species abundance	- 0.137	0.131	0.061	- 0.020	- 0.001	- 0.082	0.124	- 0.133

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Many character-states are significantly correlated: 414 of the 704 computed correlations are significant and justify multivariate analysis. The 1-2 factorial plane of the PCA conducted on the 40 x 40 contingency table based on fruit character-states shows consistent connections of these fruit character-states (Fig. 1). Collectively the first two principal components explain 54.9% of the total sample variance. The first component, which accounts for 40.2% of the total variation, reflects the importance of three character-states: 1-2 seeds (20.8% of absolute contribution), juicy soft (11.4%) and scattered (13.3%). The second axis (14.7% of the total variation) contrasts capsules (17.3% of absolute contribution) and fleshy thin tissues (15.4%) with drupes (11.7%) and unprotected fruits (9.1%).
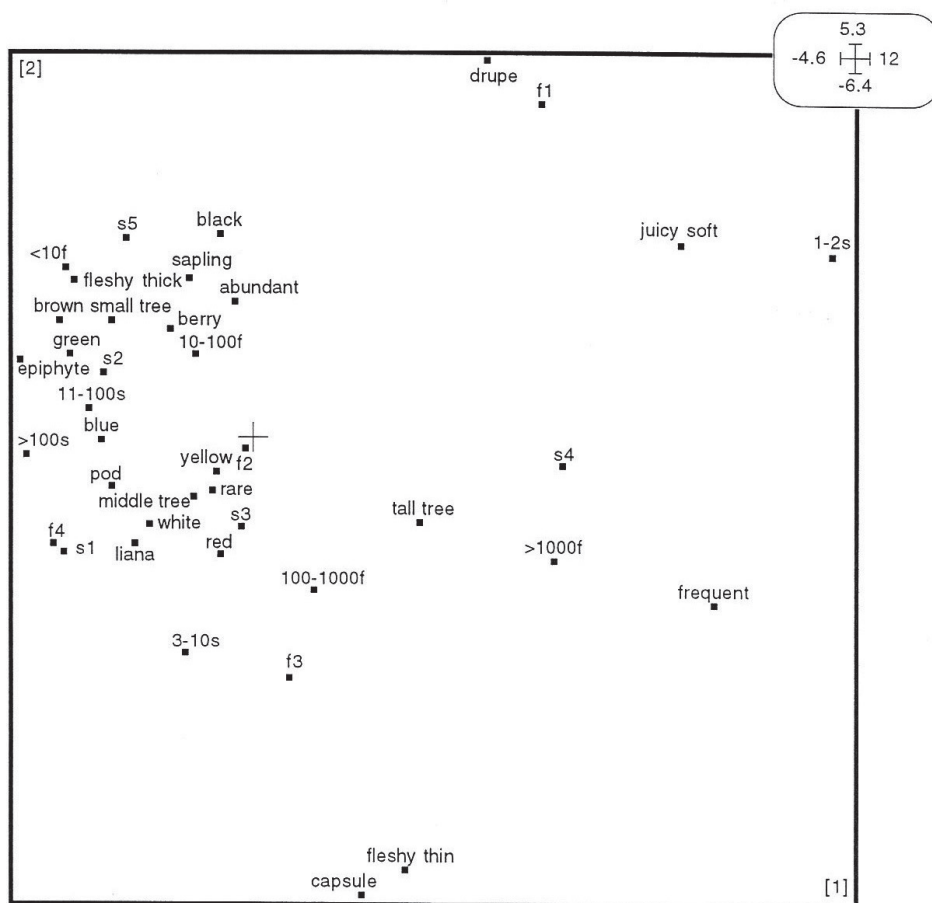
Figure 1. — Factorial plane 1-2 of the principal components analysis showing contingencies among the various fruit character-states. For abbreviations see Materials and Methods (Plant species studied). Coordinates of the axes are indicated in the rectangle at upper right corner. The cross locates the intersection of the axes. The horizontal axis (PC1) mainly stresses the importance of 1-2 seeds, juicy soft fruits of frequent plants. The vertical axis (PC2) mainly contrasts capsules and fruits with fleshy thin tissues to drupes and unprotected fruits.

The principal components reveal three main associations. First, as expected from their structure, drupe species are often unprotected (31/42 = 74%; r = 0.903, p < 0.0001, contingency table 40 x 40) and nearly always contain 1-2 seeds (41/42 = 98%; r = 0.900, p < 0.0001, contingency table 40 x 40). Second, species with soft, juicy tissue often contain 1-2 seeds (48/59 = 81%; r = 0.917, p < 0.0001, contingency table 40 x 40). Third, most capsules have thin, fleshy tissues (27/33 = 82%: fleshy thin; r = 0.956, p < 0.0001, contingency table 40 x 40).

These results are of course not a surprise. However, they show that drupes and capsules are much more distinct fruit types than pods and berries which have very overlapping characteristics (i.e., from our point of view, they differ only by the hardness of the outer fruit coat).

Pods and more particularly drupes (as expected from their definition) are associated with fewer seeds than berries and especially capsules, and tall trees are associated with the production of larger numbers of ripe fruits than smaller trees, epiphytes or lianas. High seed protection (no seed coat opened without a knife) is clearly linked to the production of few fruits. On the other hand, mass production is more associated with high seed protection (22 out of the 50 species with fruit production > 1000 have seed coats that are difficult to open) than with lack of seed protection (5 of these 50 species are unprotected).

The production of many seeds per fruit tends to be associated with little fruit protection (the two species with more than 100 seeds and seven of the nine species with 11-100 seeds show character-states f1 or f2), contrary to that of few seeds which is linked to high fruit protection (11 out of 17 species with 3-10 seeds and 21 out of 72 species with 1-2 seeds have fruits difficult to open). Fruit colour appears related to flesh type: most black or yellow fruits have soft, juicy tissues (respectively 17 of the 22 species and 15 of the 20 species), whereas most red fruits have thin, fleshy tissues (13 of the 22 species).

FRUIT SELECTION BY BIRD SPECIES

We first considered the occurrence of fruit families and species in the diet of each bird. Thirty nine plant families were identified in the diet of at least one of the four large frugivorous birds: 26 for *Crax* (with Meliaceae, Myrtaceae and Arecaceae accounting for 56% of the diet), 14 for *Penelope* (with Arecaceae and Myrtaceae totalling 66% of the diet), 19 for *Psophia* (with Lauraceae and Arecaceae representing 50% of the diet) and 18 for Tinamus (with Myristicaceae accounting for 45% of the diet). Among the 105 identified plant species 60, 45, 35 and 20, respectively, were identified in digestive tracts of *Crax*, *Psophia*, *Tinamus* and *Penelope*.

Both qualitative and quantitative distributions among the bird species of these fruiting plant species according to their characteristics (Appendices 2 and 3) illustrate significant differences in the fruit preferences of these birds.

The overall characteristics of these fruits (column Σ of Appendix 2) suggest a "general syndrome" for these four large tropical forest bird species, i.e. a dominance of red, black, yellow or white drupes and capsules, containing a few seeds in a juicy soft or fleshy thin pulp. These fruits are mainly poorly protected (68/105 = 65% being soft or easy to open) but their seeds are strongly protected (85 having seeds difficult to burst with fingernails or even very hard to cut with a knife). They come mainly from common (85 being scattered or abundant) and rather highly productive (78 produce > 100 fruits) tall trees. This "general syndrome" means that the four bird species share a somewhat overall similar frequency distribution pattern of fruit species among the various character-states. Nevertheless some differences appear between them (Appendices 2 and 3). Both cracids take more pods than the other two. The three terrestrial species ingest more red items than the arboreal *Penelope* which in turn eats more berries and more brown or yellow fruits with a more juicy soft pulp. Compared to the other bird species, *Tinamus* eats fewer yellow fruits and *Psophia* takes more fruit from rare plant species. When frequencies are expressed as percentages of either number of plant species or weight of fruit species ingested (Appendix 3), it appears that all four bird species exhibit the same dominance of fruits with eight character-states: juicy soft 1-2 hard-seeded unprotected drupes massively produced by frequent tall trees.

However, this general pattern reveals discrete associations through a multifactorial analysis based on a contingency table of dimensions 4 x 40 with frequency of fruit character-states expressed for each bird species as the number of fruit species in its diet showing this character-state. Figure 2 diagrams the 1-2 factorial plane of fruit species eaten by at least one of the four bird species in the same area and at the same seasons.
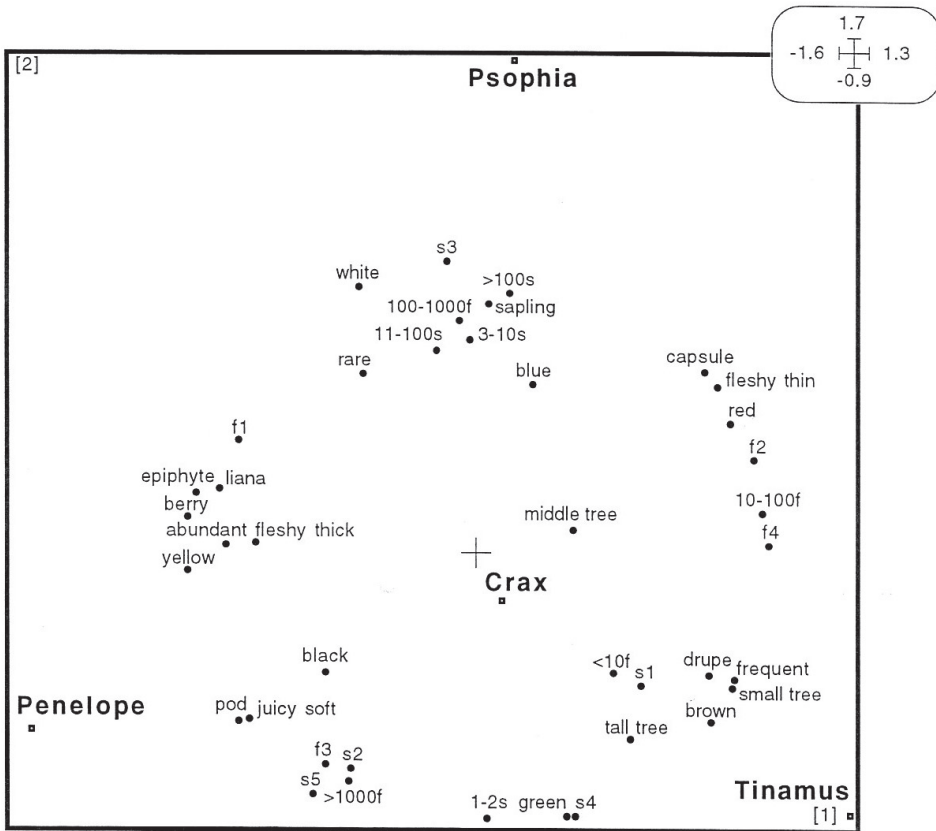
Figure 2. — Factorial plane 1-2 of the principal components analysis showing bird preference for fruit characters, based on the occurrence of plant species in the diet of the studied birds (frequencies in number of fruit species with character-state i eaten by bird species j). For abbreviations see Materials and Methods (Plant species studied). Coordinates of the axes are indicated in the rectangle at upper right corner. The cross locates the intersection of the axes. The horizontal axis (PC1) mainly contrasts easy to open with very hard fruits, yellow with brown fruits, berries with drupes and capsules, and gives also weight to epiphytes and plants producing 10-100 fruits. It contrasts *Penelope* with *Tinamus*. The vertical axis (PC2) mainly contrasts white with green fruits, and gives weight to fruits with 1-2 seeds and those with seeds difficult to cut. It contrasts *Psophia* with *Penelope* and *Tinamus*.

Fruit character-states are very differently arranged on Figure 2 compared to Figure 1: they are well distributed on a correlation circle which clearly separates the four consumers. It is particularly noteworthy that colour, fruit and seed protection, type of fruit and fruit production account for the major part of variation in the second analysis when consumers are added, suggesting that they base their choices on these criteria.

In this second analysis, the first two principal components explain 79.9% of the total variance. The first axis accounts for 43.9% of the total inertia and mainly reflects the weight (32.8%) of six character-states: two fruit protection types (easy to open: 5.1% of absolute contribution, very hard: 5.7%), one colour (yellow: 5.6%), one fruit type (berry: 5.6%), one fruit production category (10-100 fruits: 5.5%), and one biological type (epiphyte: 5.3%). The second axis accounts for 36.0% of the total inertia and stresses the importance (24.5%) of four character-states: two colours (white: 5.7%, green: 6.0%), one seed number category (1-2 seeds: 6.7%), and one seed protection level (difficult to cut: 6.1% of absolute contribution). However, on both axes, total variance is also explained by various other character-states which each contribute 3-4% to the overall variation, indicating that fruit-species choice is truly multifactorial.

The first principal component axis (Fig. 2) clearly contrasts the three terrestrial with the arboreal species; *Penelope* (57.9% of absolute contribution) is well separated from *Tinamus* (41.4%). The second axis contrasts *Psophia* (62.3% of absolute contribution) with *Tinamus* (26.3%) as well as *Penelope* (10.7%). *Crax* appears less well-discriminated (0.2% of absolute contribution to the first component, 0.7% to the second) by the character-states of its fruits, i.e. it seems to be more generalized and without clear preferences, and therefore occupies a central position in the graphical representation.

However, the factorial plane 1-2 can be split by a diagonal running from the lower left to the upper right corner and thence seed-dispersers (*Penelope* and *Psophia*) are clearly separated from seed-destroyers (*Crax* and *Tinamus*). The two terrestrial seed-destroyers, *Crax* and *Tinamus*, are weakly separated from each other by this analysis. They both exploit green fruits with few hard seeds, produced in large numbers by small trees, though *Tinamus* also shows a strong preference for frequent species producing very hard-seeded brown drupes. The seed-dispersers, arboreal *Penelope* and terrestrial *Psophia*, are well separated in this analysis; *Psophia* is associated with hard-seeded fleshy fruits, whereas *Penelope* shows a preference for yellow or black juicy soft berries and pods.

FRUIT PARTITIONING AMONG CONSUMERS

Nineteen plant species (in bold types in Appendix 1) each make up at least 5% of the fruit quantity in the diet of at least one of the bird species. Altogether, they account for 65.4% of fruit quantity and 12.6% of fruit species ingested by *Crax*, these values being, respectively, 74.5% and 16.4% for *Psophia,* 82.1% and 16.6% for *Penelope,* and 84.5% and 28.8% for *Tinamus.* Arecaceae and *Eugenia coffeifolia* (Myrtaceae) are important for these birds, particularly for *Penelope* (65% of diet) which concentrates on species both common and with heavy fruiting. One notes also the importance of *Ocotea* (Lauraceae, 32%) for *Psophia*, of *Guarea* (Meliaceae, 29.5%) for *Crax*, and of *Virola* (Myristicaceae, 44.7%) for *Tinamus*.

When the two seed-dispersers (*Penelope* and *Psophia*) are contrasted with the two seed-predators (*Crax* and *Tinamus*) some patterns emerge (cf. Appendix 3), although these patterns are sometimes different when fruit character-states are measured by the relative number of plant species (% N) or by the relative quantity of fruit (% Q) in the diet.

Dispersers and predators feed mainly on the fruits of tall trees, the trend is most pronounced with % Q than with % N. Both also tend to feed on fruits produced by frequent plant species, less on abundant ones and still less on rare ones; however the pattern is not exactly the same with % N as with % Q: for instance with % N, dispersers have in their diet almost the same percentage of rare as abundant plant species (respectively 21% and 27%) but they ingest (% Q) a low proportion (8.5%) of fruits of rare plant species. Clearly dispersers and predators feed on fruits of the various production categories of plant species with however a marked preference for high-producing species. On the other hand, with % Q, much more than predators dispersers eat fruits of high-producing plants (84% vs 58%).

With % N, dispersers and predators show the same pattern of utilization of *fruit types* but with % Q, dispersers eat predominantly drupes (77.5%) whereas predators feed as well on drupes (41%) as on capsules (42%). With % N, dispersers consume almost the same proportions of fruits with the various types of *edible tissue* as predators but, with % Q, predators eat as many juicy soft (42%) as fleshy thin fruits (47%) whereas dispersers eat mainly juicy soft fruits (62%). For the character-state *colour* with % N, dispersers tend to feed somewhat more on yellow (28%) or black (26%) fruits and much less on brown (2%) or green (2.5%) fruits whereas predators consume rather evenly fruits of the various colours with however a trend towards a preference for red (24.5%) or black (23%) fruits. With % Q, dispersers eat mainly black fruits (73%) whereas predators consume mainly red (49%) or black (24%) fruits. For the character-state *fruit protection* expressed by % N, fruit eaten by dispersers are mainly unprotected (61.5%) whereas those eaten by predators are more evenly distributed among the categories f_1 (no protection), f_2 (easy to open) and f_3 (difficult to open with fingernails). On the other hand, with % Q, fruits eaten by dispersers are predominantly unprotected (75.5%) whereas those eaten by predators are more evenly distributed among the four protection categories.

With regard to the *seed protection*, with either % N or % Q, predators eat mainly fruits with well protected seeds ($s_4 + s_5$: 75% with % N, 81% with % Q) whereas dispersers eat mainly fruits with well protected (68% with % N, 67% with % Q) or unprotected or easy to burst seeds ($s_1 + s_2$: 15% with % N, 21.5% with % Q). With regard to the *number of seeds*, dispersers as well as predators eat predominantly fruits with one or two seeds.

The third principal component analysis based on a contingency table of dimensions 4 x 40 considers the *quantitative importance* of each fruit character-state in the diet of each of the four bird species (Figure 3). The first principal component explains 53.4% of the total variance; it stresses the importance of three fruit types (drupe: 4.3% of absolute contribution, capsule: 4.6%, pod: 4.4%), three flesh types (juicy soft: 4.4%, fleshy thin: 4.6%, fleshy thick: 4.3%), two biological types (shrub: 4.3%, epiphyte: 4.5%), one fruit-protection type (unprotected: 4.4%), one fruit production character-state (< 10 fruits: 4.0%), and one seed protection level (impossible to cut: 4.0%). These 11 character-states account for 47.8% of the total inertia. Despite principal component analysis, fruit selection is still multifactorial on this axis. The second component (40.5% of the system variance) discriminates fewer character-states: unprotected seed (8.2% of absolute contribution), 3-10 seeds (8.0%), green colour (7.9%), 1-2 seeds (7.9%), very hard fruit (7.8%), and berry (7.4%).
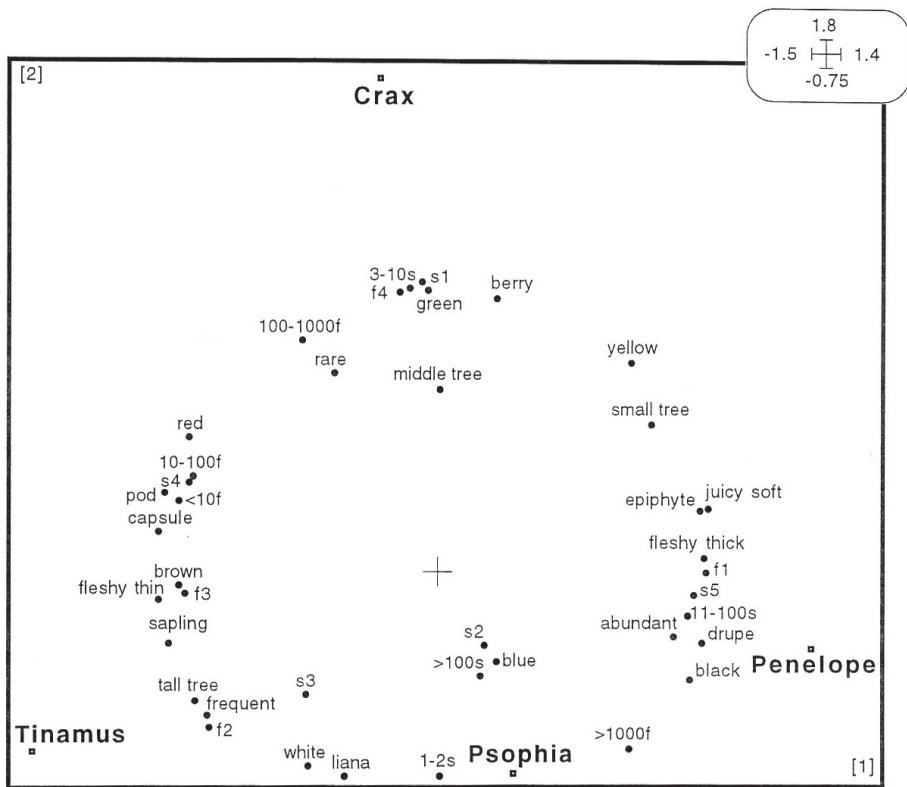
Figure 3. — Factorial plane 1-2 of the principal components analysis showing bird preference for fruit characters, based on the quantitative importance of each fruit character-state in the diet of the studied birds (frequencies in weight of fruit species with character-state i ingested by bird species j). For abbreviations see Materials and Methods (Plant species studied). Coordinates of the axes are indicated in the rectangle at upper right corner. The cross locates the intersection of the axes. The horizontal axis (PC1) mainly contrasts drupes with capsules and pods, juicy soft and fleshy thick with fleshy thin fruits, epiphytes with shrubs (saplings), unprotected with protected fruits, low with high producing plants and very protected seeds with the others. It contrasts *Penelope* with *Tinamus*. The vertical axis (PC2) mainly contrasts unprotected with protected seeds, fruits containing less than 10 seeds with the others, green fruits with the others, very hard fruits with the others and berries with the other fruit types. It contrasts *Crax* with the other three large frugivorous birds.

Figure 3 shows factorial plane 1-2 for this analysis. As in Figure 2, fruit character-states are arranged around a correlation circle, but in quite a different way that largely separates *Crax* from the other species. In this analysis fruit colour and plant production drop out while types of plant, fruit and flesh, as well as fruit and especially seed protection become important variables. Compared to the preceding analysis, terrestrial and arboreal species are here less sharply contrasted, but the two seed-destroyers (*Crax* and *Tinamus*) are very well separated in the factorial plane. Though well apart from them, the two seed-dispersers (*Psophia* and *Penelope*) show more convergent preferences. The first axis contrasts *Tinamus* (51.6% of absolute contribution) with *Penelope* (45.5%), and the second axis separates *Crax* (72.9% of absolute contribution) from *Psophia* (13.9%). Red fruits are associated with *Crax* and *Tinamus* whereas black ones are linked to *Penelope* and *Psophia*. *Crax* is also very typical in that it selects very hard fruits, containing 3-10 unprotected seeds, and among the studied birds, is also the species eating the highest proportion of berries and green fruits. *Penelope* is remarkable in its choice of juicy soft and fleshy thick drupes; unlike *Crax*, it shows a strong preference for very hard-seeded soft fruits: it eats unprotected fruits with seeds impossible to open with a knife. Arboreal *Penelope* also eats more fruits produced by epiphytes. *Tinamus* ingests hard fruits containing hard seeds; it is characterized by its choice of fruit items from capsules with fleshy thin tissue (often arils) and eats more fruits from scattered shrubs or tall trees than the other birds. *Psophia* appears more eclectic, less choosy than the other species. That is not to say there are no fruit characteristics related to this disperser, indeed as in the previous analysis, white or blue fruits appear closely related to this bird species. These fruit colours and red clearly segregate the two seed-dispersers (see Appendix 3). Its location near the discriminant character-state 1-2 seeds is mostly related to the low proportion of this variable in *Crax*'s diet. It is also the species most closely associated with fruits produced by lianas.

DISCUSSION

In our previous studies (Erard & Sabatier, 1989; Erard *et al.,* 1991; Théry *et al.,* 1992), we focused on the species composition of the diet of these four syntopic large frugivorous birds without considering the characteristics of the plant species and of the fruit that composed their diet. We present here a much better picture of how these bird species share food resources. Though we could previously conclude that in spite of some overlap these birds show important differences in the composition of their diet and thus limit interspecific competition, the question remained as to whether these differences were due to species-specific utilization of a fruit-characteristics spectrum or to mere chance fruit encounters in specific microhabitats. Though we did observe some subtle differences in the way these bird species visited the various components of the forest mosaic, our results support the hypothesis of specific fruit choice.

FRUIT CHARACTERISTICS AND CONSUMER CHOICE. CAN WE REALLY SPEAK OF FRUIT SYNDROMES?

As pointed out in the introduction, fruit choice by frugivores is highly multifactorial. We could not study all factors possibly involved. However, with nine easily quantifiable variables represented by 40 character-states, we could expect multifactorial analyses to detect associations between variables and/or character-states that can be interpreted as fruit-character syndromes linked to particular consumers. With the same small number of variables and character-states, such syndromes were indeed detected in a study of forest frugivores in Gabon (Gautier-Hion *et al.,* 1985; see also Mitani, 1999 in Cameroon): bird-monkey and ruminant-rodent-elephant syndromes, which could as well have been interpreted as arboreal and terrestrial frugivore syndromes because all frugivorous bird species studied were arboreal as were the monkeys, not terrestrial like the other mammals.

The present results show that the fruit diet of each of the four bird species we studied can be defined by a simple set of characters. Thus, the arboreal seed-disperser *Penelope* seeks black or yellow, juicy soft berries and drupes from relatively frequent and very highly productive tall

trees, lianas and shrubs. These fruits are not particularly protected and contain one or a few protected seeds. On the other hand, the terrestrial seed-predator *Crax* looks mainly for red, yellow or black juicy soft or fleshy fruits from relatively scattered or abundant shrubs, small or tall trees, producing many fruits. These fruits contain 1-2 very well protected seeds and many of them have a tough seed coat. The terrestrial seed-disperser *Psophia* searches for moderately tough-coated, yellow, black, white, blue or red, juicy soft or fleshy thin drupes but also berries and fruit items from capsules with well-protected seeds; other plant characteristics do not appear important though one may note the relative importance of rare fruiting plant species as well as rare fruit characters in the diet of this bird species. Such rare fruit characters are well exemplified by *Margarita nobilis*, a small tree, producing capsules from which iridescent blue endocarps drop to the forest floor where they may stay intact for several days. The terrestrial seed-predator *Tinamus* eats drupes and fruit items from capsules from a large array of colours, including green and brown; these fruits are rather well-protected, juicy soft or fleshy thin, and come from relatively frequent and highly productive tall and smaller trees that contain 1-2 very well protected seeds.

Though the above definitions indicate what kind of fruit each bird species eats, they do not allow a straightforward classification of fruit species into species-specific consumer categories. It must also be said that a real detection of syndromes requires a reference to the whole array of fruit species available in the plant community to see if the pattern of the fruits consumed is actually a non-random subset of the total morpho-space of the whole fruit community. Although we could not do that it is interesting to note that the three main primates studied at the same place and time (Guillotin *et al.*, 1994) consumed the fruits of 107 plant species belonging to 47 families but only 31 of these species belonging to 27 families were also eaten by the four large frugivorous birds. The fruits consumed by monkeys were mainly berries or cacaopod-like, small to large, orange-yellow, orange or varied intensities of red, with moderately hard seeds, and were thus different from those eaten by the birds. With our present knowledge (based on our data on birds and on those on monkeys and terrestrial mammals by Guillotin, 1981; Henry, 1987, 1994; Guillotin *et al.*, 1994), the proportion of fruits in their diet known to be eaten exclusively by each of these bird species, respectively, is 5% (3 species) for *Penelope*, 11% (18 species) for *Crax*, 28% (18 species) for *Psophia*, and 42% (10 species) for *Tinamus*. This suggests that although our data do not actually allow us to conclude that syndromes exist with particular fruit traits linked exclusively to particular bird species, the hypothesis is however worth further study with a larger number of fruit characters (placed in a phylogenetic perspective, see Fischer & Chapman, 1993; Jordano, 1995) and at larger frugivore-community scale (see also Chapman & Chapman, 2002; Lord *et al.*, 2002).

We have indicated above that, for each of these large frugivorous birds, the fruits of a few plant families account for an important proportion of the diet (in quantity of ingested fruits not in number of plant species), and that these families are different from one bird species to the other. This suggests that these birds may actually sample different higher taxa of the fruits available, and that the variation in the multivariate patterns for the fruits might be a by-product of phylogenetic effects on the fruit traits.

ARBOREAL VS TERRESTRIAL CONSUMERS AND SEED-DISPERSERS VS SEED-PREDATORS

The analysis based on whether bird species i eats fruit species j (Figure 2), shows that fruit character-states are linked in such a way that particular sets of them can be clearly associated with *Penelope, Psophia* or *Tinamus*. These three species differ sharply from each other and also from *Crax* in their fruit selection; *Tinamus* is however closer to *Crax* than to the others. *Crax* appears also more generalist in its fruit choice. In the same analysis, sets of character-states with highest absolute contribution (see above in the results) can also be interpreted as making distinct clusters linked either with seed-dispersers (upper left half of Figure 2, from PC_1^- to PC_2^+) or with seed-predators (lower right corner of Figure 2, PC_1^+, PC_2^-). The analysis also contrasts the arboreal species (*Penelope* in lower left corner of Figure 2) with the terrestrial ones. However this second contrast is a little less clear-cut than the previous one. This suggests that if there is a fruit syndrome, it is based more on the contrast between seed dispersal and

seed predation than on the opposition of arboreal to terrestrial consumers. Indeed, the analysis based on the quantities of fruit eaten (Figure 3) gives more weight to the distinction between seed-dispersers and seed-predators than to that between arboreal and terrestrial consumers in the definition of fruit-character sets.

When quantities of ingested fruit are considered, every bird species is then clearly linked to a particular set of fruit character-states, even *Crax*. This suggests that before reaching firm conclusions about eventual fruit character syndromes a quantification of frugivore diets is needed (see also Poulsen *et al.*, 2002). Furthermore, comparative studies in different regions would also be necessary because this quantification can depend on local conditions (i.e. fruit and frugivorous species present and interacting).

SOME COMMENTS ON FRUIT SYNDROMES AND COADAPTIVE VS COEVOLUTIONARY SYSTEM

Coevolution means reciprocal evolutionary change between interacting species (Thompson, 1994, 2002). Numerous studies show that many plant traits have possibly evolved in response to consumers though other evolutionary pathways can be envisioned. However, the evolutionary response of the consumers to the interaction with plants is not yet clear and is further complicated by the fact that many "frugivores" include a more or less important part of animal prey in their diet; this asymmetry in specialization patterns has led to the catchall designation of diffuse coevolution (on these rather coarse ecological and evolutionary interplays between plants and frugivores see Howe, 1984; Herrera, 1985; Wheelwright, 1988; Fleming, 1991; Jordano, 1992; Mazer & Wheelwright, 1993; Cipollini, 2000; Chapman & Chapman, 2002).

Discussions of coevolutionary aspects of animal-plant interactions often mainly rely on relations between fruiting plants and their seed-dispersers. The theoretical framework is that of a trade-off where the plant pays an energetically rewarding, nutrient-rich fruit to satisfy the needs and preferences of its seed-disperser which is itself constrained by its morphology and physiology. However these discussions often dismiss the fate of seeds, seedlings, saplings and all stages leading to the adult reproductive plant which is the real transmitter of the selected genetic traits (see also Jordano & Herrera, 1995). Time elapsed from seed dispersal to reproducing plant is usually long and may include important changes in the composition and organization of the frugivore assemblages and even of the plant community (see e.g. Herrera, 1998). In other words we witness a theatre play where the actors modify the scenery set up by the actors of the preceding play and which will be used and modified by the actors of the following play. Both scenery and actors change but not at the same pace and time scale (for discussions of factors limiting coevolution see Herrera, 1985, 1986, 1998; Wheelwright, 1988; Fischer & Chapman, 1993; Chapman & Chapman, 2002; Hulme & Benkman, 2002; Lord *et al.*, 2002; Thompson, 2002).

Another problem is that syndromes are defined with reference to the dispersers but plants have characteristics that predispose them to a particular dispersal mode but may be dispersed in a complete different way (see Williams & Guries, 1994). Moreover, at least some fruit traits (e.g. colour) may reflect several functions (Willson &Thompson, 1982; Wheelwright & Janson, 1985; Cipollini & Levey, 1991; Fisher & Chapman, 1993). Fruit traits may be influenced by physical variables depending on environmental constraints and could have evolved also in response to selection on taxon-specific genetically correlated traits such as stem, flower or leaf variables (Primack, 1987; Herrera, 1992b). Constraints on fruit traits selection may be highly diverse: e.g. location and exposure of the fruit may depend on the flower and inflorescence which may have been selected for by pollinators and by physical variables, and accumulation of nutrients in the seed may be controlled by germination needs as well as by anti-predator (before, during and after dispersal) or consumer-attractive requirements. Fruit traits may also have evolved not only directly in response to the effect of consumers, either seed-dispersers or seed-predators, but also indirectly to attract predators and parasites of herbivores (third trophic level, see Marquis & Whelan, 1996); indeed some traits such as pulpiness may have originated primarily from defensive responses to herbivores rather than as a means to enhance seed dispersal (Mack, 2000; see also Erard & Théry, 1994). The importance and effects of potentials

in vegetative reproduction of plants, e.g. cloning, stem suckers, runners, budding, as well as developmental mechanisms responsible for the regulation of biomass allocation patterns during plant development which contribute to the dilution of coevolutionary patterns are usually neglected in the discussions of plant-animal interactions.

Furthermore, past history and phylogeny of the plants (Herrera, 1992b; Janson, 1992; Fischer & Chapman, 1993; Jordano, 1995; Cipollini *et al*., 2002) are important to consider: what we observe nowadays evolved long ago and similarities may be attributable to common ancestry rather than to convergent or parallel evolutionary changes. Many modern plant families are known from early Eocene and drupe-like fruits may have already been present in the late Cretaceous (Friis *et al.,* 1987; see also Tiffney, 1986; Howe & Westley, 1988; Eriksson *et al.,* 2000). Tropical forests have fluctuated very much both in distribution and composition during their history. Bottlenecks existed corresponding to restrictions in range (refugia) during which plant species had to adapt both to ecological conditions that modified and reduced their distributions and to changes in the assemblages of their consumers (e.g. herbivores, nectarivores, frugivores). During these bottlenecks surviving plants were under ecological constraints which forced them to develop morpho-anatomical and physiological structures and particularities that minimized risks of mortality and extinction (e.g. reinforced protection of their seeds against predators and attractive features for dispersers).

CONCLUSIONS

In respect of our first question on whether these four bird species differ in their fruit choice, each searching for fruits with particular characteristics, the results of the present study show that these frugivores share a staple diet composed of coloured, fleshy and not well-protected fruits containing a few well-protected seeds, and coming from plants with high standing crop. However, it appears that each of the four syntopic large frugivorous birds presents some specificity in the characteristics of the fruits it eats, even if the results do not permit to conclude that fruit traits are evolutionary determined by seed-dispersers as implied by the concept of fruit syndrome. Indeed, these results help to define sets of fruit character-states linked to specific consumers with distinct traits being associated with ingestion by a seed-predator or a seed-disperser. There is also a possible separation between arboreal and terrestrial consumption.

This leads to our second question on what do fruit traits reflect in these circumstances: mutualism or interactions between a predator and its "prey"? The two dispersers *Penelope* and *Psophia* eat more coloured, fleshier, and often multi-seeded fruits than the two predators *Crax* and *Tinamus* which select fruits with well-protected and often single seeds. We identify mutualism in the interactions between fruiting plants and *Penelope* and *Psophia*: plants take benefit from the dispersal of their seeds whereas birds benefit from the pulp of the fruits. Conversely and though at least *Crax* may be a mutualist for some plants whose small seeds pass unaltered through its digestive tract, we consider that the interactions between fruiting plants and *Crax* and *Tinamus* are not mutualism: obviously birds benefit from the whole fruit (pulp and seeds) whereas plants developed hard-coated seeds requiring a consumer equipped with a secretory crop to soften them and a strong muscular gizzard with ingested grit to grind them. Plant defences may be chemically strengthened (e.g. by secondary metabolites) but this subject remains to be explored in the present case.

Coming now to our third question about what can be inferred of the role each bird species plays in forest dynamics and of the effects of fruit production variability on populations of these birds, obviously answers can be no more than highly speculative. In the case of important fruit scarcity, these bird species except *Psophia* which feeds also on animal prey, would have to move away or would otherwise suffer an increased mortality rate. Because of the existence of coarse associations between fruit character-states and specific consumers, the importance of this frugivorous bird assemblage for the regeneration processes of forest dynamics cannot be dismissed. Because of important differences in their diet and foraging behaviour, *Penelope* and *Psophia* are unlikely to replace each other in their roles as seed-dispersers; likewise, *Crax*

and *Tinamus* may act complementarily (they select different plant families) on the reduction of seed density under the fruiting plants.

ACKNOWLEDGEMENTS

REFERENCES

BEEHLER, B.M.(1981). — Ecological structuring of forest bird communities in New Guinea. *Monogr. Biol.*, 42: 837-861.

BROSSET, A. (1990). — A long term study of the rain forest birds in M'Passa (Gabon). Pp. 259-274, *in*: Keast, A. (ed.). *Biogeography and ecology of forest bird communities*. SPB Academic Publishing bv, The Hague.

BROSSET, A. & ERARD, C. (1986). — Les oiseaux des régions forestières du Nord-Est du Gabon. Vol. 1: Ecologie et comportement des espèces. *Rev.Ecol. (Terre Vie)*, suppl. 3: 1-297.

CHAPMAN, C.A. & CHAPMAN, L.J. (2002). — Plant-animal coevolution: is it thwarted by spatial and temporal variation in animal foraging? Pp. 275-290, *in*: D.J. Levey, W.R. Silva & M. Galetti (eds) *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI Publishing, Oxon & New York.

CHARLES-DOMINIQUE, P. (2001). — Relationships between seed dispersal and behavioural ecology. Pp. 191-196, *in*: F. Bongers, P. Charles-Dominique, P.-M. Forget & M. Théry (eds) *Nouragues. Dynamics and plant-animal interactions in a neotropical rainforest*. Kluwer Academic Publishers, Dordrecht, Boston & London.

CHARLES-DOMINIQUE, P, ATRAMENTOWICZ, M., CHARLES-DOMINIQUE, M., GÉRARD, H., HLADIK, A., HLADIK, C.M. & PRÉVOST, M.-F. (1981). — Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. *Rev. Ecol. (Terre Vie)*, 35: 341-435.

CHEN, J., FLEMING, T.H., ZHANG, L., WANG, H. & LIU, Y. (2004). — Patterns of fruit traits in a tropical rainforest in Xishuangbanna, SW China. *Acta Oecol.*, 26: 157-164.

CIPOLLINI, M.L. (2000). — Secondary metabolites of vertebrate-dispersed fruits: evidence for adaptive functions. *Rev. Chilena Hist. Nat.*, 73: 421-440.

CIPOLLINI, M.L., BOHS, L.A., MINK, K., PAULK, E. & BÖHNING-GAESE, K. (2002). — Secondary metabolites of ripe fleshy fruits: ecology and phylogeny in the genus *Solanum*. Pp. 111-128, *in*: D.J. Levey, W.R. Silva & M. Galetti (eds) (2002). — *Seed dispersal and frugivory: Ecology, evolution and conservation*. CABI Publishing, Oxon & New York.

CIPOLLINI, M.L. & LEVEY, D.J. (1991). — Why some fruits are green when they are ripe: carbon balance in fleshy fruits. *Oecologia* (Berlin), 88: 371-377.

CIPOLLINI, M.L. & LEVEY, D.J. (1997). — Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *Am. Nat.,* 150: 346-372.

CURRAN, L.M. & WEBB, C.O. (2000). — Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecol. Monogr.*, 70: 129-148.

DEBUSSCHE, M. & ISENMANN, P. (1989). — Fleshy fruit variables and the choices of bird and mammal seed-dispersers in a Mediterranean region. *Oikos*, 56: 327-338.

DELACOUR, J. & AMADON, D. (2004). — *Curassows and related birds*. Updated by J. del Hoyo & A. Motis. Lynx Edicions & The National Museum of Natural History, Barcelona & New York.

DOWSETT-LEMAIRE, F. (1988). — Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. *Rev. Ecol. (Terre Vie),* 43: 251-285.

ERARD, C. (1986). — Richesse spécifique de deux peuplements d'oiseaux forestiers équatoriaux: une comparaison Gabon-Guyane. *Mém. Mus. Nat. Hist. Nat.*, A (Zoologie), 132: 53-66.

ERARD, C. (1989). — Bird community structure in two rainforests: Africa (Gabon) and South America (French Guiana) - A comparison. Pp. 89-122, *in*: M.L. Harmelin-Vivien & F. Bourlière (eds). *Vertebrates in complex tropical systems*. Ecological Studies 69. Springer-Verlag, New York, Berlin, Heidelberg, London, Paris & Tokyo.

ERARD, C. & SABATIER, D. (1989). — Rôle des oiseaux frugivores terrestres dans la dynamique forestière en Guyane française. *Proc. Int. Ornith. Congr.*, 19: 803-815.

ERARD, C. & THÉRY, M. (1994). — Frugivorie et ornithochorie en forêt guyanaise: l'exemple des grands oiseaux terrestres et de la Pénélope marail. *Alauda,* 62: 27-31.

ERARD, C. & THÉRY, M. (2001). — Vegetarian species in the bird community with an emphasis on frugivory and seed dispersal. Pp. 233-241, *in*: F. Bongers, P. Charles-Dominique, P.-M. Forget & M. Théry (eds). *Nouragues. Dynamics and plant-animal interactions in a neotropical rainforest.* Kluwer Academic Publishers, Dordrecht, Boston & London.

ERARD, C., THÉRY, M. & SABATIER, D. (1989). — Régime alimentaire de *Rupicola rupicola* (Cotingidae) en Guyane française. Relations avec la frugivorie et la zoochorie. *Rev. Ecol. (Terre Vie),* 44: 47-74.

ERARD, C., THÉRY, M. & SABATIER, D. (1991). — Régime alimentaire de *Tinamus major* (Tinamidae), *Crax alector* (Cracidae) et *Psophia crepitans* (Psophiidae) en forêt guyanaise. *Gib. Faune sauv.*, 8: 183-210.

ERIKSSON, O., FRIIS, E.M. & LOFGREN, P. (2000). — Seed size, fruit size, and dispersal systems in angiosperms from the early Cretaceous to the late Tertiary. *Am. Nat.*, 156: 47-58.

ESTRADA, A. & FLEMING, T.H. (eds) (1986). — *Frugivores and seed dispersal*. Dr W Junk Publishers, Dordrecht.

FISCHER, K.E. & CHAPMAN, C.A. (1993). — Frugivores and fruit syndromes: differences in patterns at the genus and species level. *Oikos*, 66: 472-482.

FLEMING, T.H. (1991). — Fruiting plant-frugivore mutualism: The evolutionary theater and the ecological play. Pp. 119-144, *in*: P.W. Price, T.M.Lewinsohn, G.W. Fernandes & W.W. Benson (eds). *Plant-animal interactions: Evolutionary ecology in tropical and temperate regions*. John Wiley and Sons, Inc., Chichester, New York, Weinheim, Brisbane, Singapore & Toronto.

FLEMING, T.H., BREITWISCH, R. & WHITESIDES, G.H. (1987). — Patterns of tropical vertebrate frugivore diversity. *Ann. Rev. Ecol. Syst.,* 18: 91-109.

FLEMING, T.H. & ESTRADA, A. (eds) (1993). — *Frugivory and seed dispersal: Ecological and evolutionary aspects.* Advances in vegetation science 15. Reprinted from *Vegetatio* 107/108. Kluwer Academic Publishers, Dordrecht, Boston & London.

FORESTA, H. DE, CHARLES-DOMINIQUE, P., ERARD, C. & PRÉVOST M.-F. (1984). — Zoochorie et premiers stades de la régénération naturelle après coupe en forêt guyanaise. *Rev. Ecol. (Terre Vie),* 39: 369-400.

FORGET, P.-M., LAMBERT, J.E., HULME, P.E. & VANDER WALL, S.B. (eds) (2005). — *Seed fate. Predation, dispersal and seedling establishment.* CABI Publishing, Wallingford, UK & Cambridge, USA.

FRIIS, E.M., CHALONER, W.G. & CRANE, P.R. (eds) (1987). — *The origins of Angiosperms and their biological consequences*. Cambridge University Press, Cambridge.

FRANKIE, G.W., BAKER, H. G. & OPLER, P.A. (1974). — Comparative phenological studies of trees in tropical lowland wet and dry forest sites of Costa Rica. *J. Ecol.,* 63: 881-919.

FUENTES, M. (1994). — Diets of fruit-eating birds: what are the causes of interspecific differences? *Oecologia*, 97: 134-142.

GABRIEL, K.R. (1971). — The biplot graphical display of matrices with application to principal component analysis. *Biometrika*, 58: 453-467.

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

GENTRY, A.H. (1982). — Patterns of Neotropical plant species diversity. *Evol. Biol.,* 15: 1-84.

GUILLOTIN, M. (1981). — *Données écologiques sur les petits rongeurs forestiers terrestres de Guyane française.* Thèse 3ᵉ Cycle, Université de Montpellier.

GUILLOTIN, M., DUBOST, G. & SABATIER, D. (1994). — Food choice and food competition among the three major primate species of French Guiana. *J. Zool.*, 233: 551-579.

HENRY, O. (1994). — Saisons de reproduction chez trois Rongeurs et un Artiodactyle en Guyane française, en fonction des facteurs du milieu et de l'alimentation. *Mammalia,* 58: 183-200.

HENRY, O. (1997). — The influence of sex and reproductive state on diet preference in four terrestrial mammals of the French Guianan rain forest. *Canad. J. Zool*., 75: 929-935.

HERRERA, C.M. (1985). — Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos,* 44: 132-141.

HERRERA, C. M. (1986). — Vertebrate-dispersed plants: why they don't behave the way they should. Pp. 5-18, *in*: A. Estrada, & T.H. Fleming (eds). *Frugivores and seed dispersal*. Junk, Dordrecht.

HERRERA, C.M. (1992a). — Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents. *Ecology*, 73: 1832-1841.

HERRERA, C.M. (1992b). — Historical effects and sorting processes as explanations for contemporary ecological patterns: variable syndromes in Mediterranean woody plants. *Am. Nat.,* 140: 421-446.

HERRERA, C.M. (1998). — Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol. Monogr*., 68: 511-538.

HERRERA, C.M. (2002). — Seed dispersal by vertebrates. Pp. 185-208, *in*: C.M.Herrera & O. Pellmyr (eds). *Plant-animal interactions. An evolutionary approach*. Blackwell Publishing, Oxford, Malden, Victoria & Berlin.

HERRERA, C.M.& PELLMYR, O. (eds). (2002). — *Plant-animal interactions. An evolutionary approach*. Blackwell Publishing, Oxford, Malden, Victoria & Berlin.

Hilty, S.L. (1980). — Flowering and fruiting in a premontane rain forest in Pacific Columbia. *Biotropica*, 12: 292-306.

Howe, H.F. (1984). — Constraints on the evolution of mutualism. *Am. Nat.,* 123: 764-777.

Howe, H.F. (1986). — Seed dispersal by fruit-eating birds and mammals. Pp. 123-190, *in*: D.R. Murray (ed.). *Seed dispersal*. Academic Press, New York.

Howe, H.F. & Westley, L.C. (1988). — *Ecological relationships of plants and animals*. Oxford University Press, New York, Oxford.

Hulme, P.E. & Benkman, C.W. (2002). — Granivory. Pp. 132-154, *in*: C.M. Herrera & O. Pellmyr (eds). *Plant-animal interactions. An evolutionary approach*. Blackwell Publishing, Oxford, Malden, Victoria & Berlin.

Janzen, D.H. (1983). — Dispersal of seeds by vertebrates guts. Pp. 232-262, *in*: D.J. Futuyama & M. Slatkin (eds*). Coevolution*. Sinauer Associates, Sunderland.

Johnson, R.A. & Wichern, D.W. (1992). — *Applied multivariate statistical analysis*. 3rd ed. Prentice-Hall, Englewood Cliffs, NJ, USA.

Jordano, P. (1987). — Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymetries, and coevolution. *Am. Nat.*, 129: 657-677.

Jordano, P. (1992). — Fruits and frugivory. Pp. 105-151, *in*: M. Fenner (ed.). *Seeds: The ecology of regeneration in natural plant communities*. CAB International, London.

Jordano, P. (1995). — Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *Am. Nat.*, 145: 163-191.

Jordano, P. & Herrera, C.M. (1995). — Shuffling the offspring: Uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience*, 2: 230-237.

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, Université de Tours.

Karr, J. R. (1989). — Birds. Pp. 401-416, *in*: H. Lieth & M.J.A. Werger (eds). *Tropical rain forest ecosystems*. Elsevier Scientific Publishing Company, Amsterdam.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. (2002). — Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, 133: 559-572.

Larue, M., Ringuet, S., Sabatier, D. & Forget, P.-M. (2002). — Fruit richness and seasonality in a fragmented landscape of French Guiana. *In*: P.-M.Forget (coord.). *Fragmentation de la forêt tropicale humide: le barrage de Petit Saut, rivière Sinnamary, Guyane française. Rev. Ecol. (Terre Vie),* suppt 8: 39-57.

Levey, D.J., Moermond, T.C. & Denslow, J.S. (1994). — Frugivory: an overview. Pp. 282-294, *in*: L.A. McDade, K.S. Bawa, H.A. Hespenheide & G.S. Hartshorn (eds). *La Selva. Ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago & London.

Levey, D.J., Silva, W.R. & Galetti, M.(eds) (2002). — *Seed dispersal and frugivory: Ecology, evolution and conservation*. CABI Publishing, Oxon & New York.

Lord, J.M., Markey, A.S. & Marshall, J. (2002). — Have frugivores influenced the evolution of fruit traits in New Zealand? Pp. 55-68, *in*: D.J. Levey, W.R. Silva & M. Galetti (eds) (2002). *Seed dispersal and frugivory: Ecology, evolution and conservation*. CABI Publishing, Oxon & New York.

Mack, A.L. (2000). — Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? *J. Biosci.,* 25: 93-97.

Marquis, R.J. & Whelan, C. (1996). — Plant morphology and recruitement of the third trophic level: subtle and little-recognized defenses? *Oikos*, 75: 330-334.

Maury-Lechon, G. & Poncy, O. (1986). — Dynamique forestière sur six hectares de forêt dense humide de Guyane française, à partir de quelques espèces de forêt primaire et de cicatrisation. *Mém. Mus. Nat. Hist. Nat.,* A (Zoologie), 132: 211-242.

Mazer, S.J. & Wheelwright, N.T. (1993). — Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evol. Ecol.,* 7: 556-575.

Mitani, M. (1999). — Does fruiting phenology vary with fruit syndrome? An investigation on animal-dispersed tree species in an evergreen forest in south-western Cameroon. *Ecol. Res.,* 14: 371-383.

Pijl, L. van der (1982). — *Principles of dispersal in higher plants*. Springer, Berlin, Heidelberg & New York.

Poulsen, J.R., Clark, C.J., Connor, E.F. & Smith, T.B. (2002). — Differential resource use by primates and hornbills: implication for seed dispersal. *Ecology*, 83: 228-240.

Prévost, M.-F. (1983). — Les fruits et les graines des espèces végétales pionnières de Guyane. *Rev. Ecol. (Terre Vie),* 38: 121-145.

Primack, R. (1987). — Relationships among flowers, fruits, and seeds. *Ann. Rev. Ecol. Syst.*, 18: 409-430.

Robinson, G.R. & Handel, S.N. (1993). — Forest restoration on a closed landfill: rapid addition of new species by bird dispersal. *Cons. Biol.,* 7: 271-278.

Robinson, S.K., Terborgh, J. & Munn, C.A. (1990). — Lowland tropical forest bird communities of a site in Western Amazonia. Pp. 229-258, *in*: Keast, A. (ed.), *Biogeography and ecology of forest bird communities*. SPB Academic Publishing bv, The Hague.

SABATIER, D. (1983). — *Fructification et dissémination en forêt guyanaise. L'exemple de quelques espèces ligneuses.* Thèse 3ᵉ Cycle, Université de Montpellier.

SABATIER, D. (1985). — Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Rev. Ecol. (Terre Vie),* 40: 289-320.

SHERMAN, P.T. (1991). — *The ecology and social behavior of the White-winged Trumpeter* (Psophia leucoptera). Ph.D. thesis, University of California, Davis.

SHERMAN, P.T. (1996). — Family Psophiidae (Trumpeters). *In*: J. del Hoyo, A. Elliott & J. Sargatal, (eds). *Handbook of the birds of the world. Vol. 3. Hoatzin to Auks*. Lynx Edicions, Barcelona.

STILES, F.G. (1985). — On the role of birds in the dynamics of Neotropical forests. Pp. 49-59, *in*: A.W. Diamond & T.E. Lovejoy (eds). *Conservation of tropical forest birds*. ICBP Technical paper n°4, Cambridge.

TERBORGH, J. (1980). — Causes of tropical species diversity. *Proc. Int. Ornith. Congr.*, 17: 955-961.

TER BRAAK, C.J.F. (1983). — Principal components biplots and alpha and beta diversity. *Ecology*, 64: 454-462.

THÉRY, M., ERARD, C. & SABATIER, D. (1992). — Les fruits dans le régime alimentaire de *Penelope marail* (Aves, Cracidae) en forêt guyanaise: frugivorie stricte et sélective? *Rev.Ecol. (Terre Vie),* 47: 383-401.

THÉRY, M. & LARPIN, D. (1993). — Seed dispersal and vegetation dynamics at a cock-of-the-rock's lek in the tropical forest of French Guiana. *J. Trop. Ecol.,* 9: 109-116.

THIOLLAY, J.-M., JULLIEN, M., THÉRY, M. & ERARD, C. (2001). — The avian community: an overview of species composition and guild structure. Pp. 129-141, *in*: F. Bongers, P. Charles-Dominique, P.-M. Forget & M. Théry (eds). *Nouragues. Dynamics and plant-animal interactions in a neotropical rainforest.* Kluwer Academic Publishers, Dordrecht, Boston & London.

THOMPSON, J. N. (1994). — *The coevolutionary process*. The University of Chicago Press, Chicago & London.

THOMPSON, J.N. (2002). — Plant-animal interactions: future directions. Pp. 236-247, *in*: C.M. Herrera & O. Pellmyr (eds). *Plant-animal interactions. An evolutionary approach*. Blackwell Publishing, Oxford, Malden, Victoria & Berlin.

TIFFNEY, B.H. (1986). — Evolution of seed dispersal syndromes according to the fossil record. Pp. 273-305, *in*: D.R. Murray (ed.). *Seed dispersal*. Academic Press, London, New York & Sydney.

TOSTAIN, O., DUJARDIN, J.-L., ERARD, C. & THIOLLAY, J.-M. (1992). — *Oiseaux de Guyane*. Société d'Etudes Ornithologiques, Paris.

WENNY, D.G. (2000). — Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol. Monogr.,* 70: 331-351.

WHEELWRIGHT, N.T. (1988). — Four constraints on coevolution between plants and their seed-dispersers: a tropical case study. *Proc. Int. Ornith. Congr.,* 19: 827-845.

WHEELWRIGHT, N.T. & JANSON, C.H. (1985). — Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.,* 126: 777-799.

WILLIAMS, C.F. & GURIES, R.P. (1994). — Genetic consequences of seed dispersal in three sympatric forest herbs. I. Hierarchical population-genetic structure. *Evolution,* 48: 791-805.

WILLSON, M.F. (1986). — Avian frugivory and seed dispersal in eastern North America. *Curr. Ornith.,* 3: 223-279.

WILLSON, M.F., IRVINE, A.K. & WALSH, N.G. (1989). — Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica,* 21: 133-147.

WILLSON, M.F. & THOMPSON, J.N. (1982). — Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are "green". *Canad. J. Bot.,* 60: 701-713.

YUMOTO, T. (1999). — Seed dispersal by Salvin's curassow, *Mitu salvini* (Cracidae), in a tropical forest of Columbia: direct measurements of dispersal distance. *Biotropica*, 31: 654-660.

ZANG, S.Y. (1994). — *Utilisation de l'espace, stratégies alimentaires et rôle dans la dissémination des graines du singe capucin* Cebus apella *(Cebidae, Primates) en Guyane française*. Thèse, Université de Paris VI.

APPENDIX 1

List and characteristics of plant species whose fruit are eaten by the four large frugivorous bird species

% diet = percentage of weight of drained plant species in the fruit diet of each considered bird species.

Growth form: SA = shrub (or sapling) or low-climbing liana; ST = small tree; MT = middle understory tree; EP = epiphyte; LI = liana reaching canopy; TT = tall tree (canopy or emergent tree).

Fruit type: BE = berry-like; DR = drupe-like; CA = dehiscing capsule; PO = pod-like (non dehiscing cacao-pod-like capsule).

Type of edible tissue: JS = juicy soft; FT = fleshy thin; FK = fleshy thick.

Colour of fruit or ingested item: BL = black or dark purple; YE = yellow; BR = brown; RE = red; BU = blue; GR = green; WH = white.

Fruit protection: f1 = no protection; f2 = easy to open; f3 = difficult to open with fingernails; f4 = can only be open with a knife.

Seed protection: s1 = no protection; s2 = easy to burst; s3 = difficult to burst with fingernails; s4 = can only be parted with a knife; s5 = cannot be cut with a knife.

Seed number: a = 1-2; b = 3-10; c = 11-100; d = > 100.

Available fruit production: a = < 10; b = 10-100; c = 100-1000; d = > 1000.

Species abundance: a = rare; b = frequent; c = abundant.

Names in bold cases: ≥ 5% of the fruit quantity in the diet of at least one of the bird species.

Plant species	% in diet				Life Form	Fruit Type	Flesh Type	Fruit Colour	Fruit Protec.	Seed Protec.	Seed Number	Fruit Prod.	Species Abund.
	Crax	*Penelope*	*Psophia*	*Tinamus*									
Annonaceae													
Duguetia cf. *eximia* Diels				0.30	ST	DR	JS	BR	f2	s4	c	a	b
Duguetia sp 1	3.60			0.07	ST	DR	JS	BR	f2	s4	a	a	b
Ephedranthus guianensis R.E. Fries	2.91				MT	DR	JS	BL	f2	s4	a	b	a
Guatteria sp 1	0.01			2.42	ST	DR	JS	BL	f2	s4	a	c	b
Guatteria sp 2	0.38	8.03		8.89	TT	DR	JS	BL	f2	s4	a	d	b
Unonopsis guatterioides (A. de Candolle) R.E. Fries	0.14				ST	DR	JS	BL	f2	s4	a	c	c
Xylopia nitida Dunal	0.01				TT	CA	FT	WH	f2	s4	b	d	c
Xylopia sp 1			0.03		TT	CA	FT	WH	f2	s4	b	d	b
Araliaceae													
Oreopanax capitatum Decaisne & Planchon	0.01				EP	BE	JS	WH	f1	s2	b	d	a
Arecaceae													
Bactris acanthocarpoides Barbosa Rodrigues	7.08		0.13	0.49	ST	DR	FK	RE	f1	s5	a	b	c
Bactris cf. gastoniana Barbosa Rodrigues	0.02			6.65	SA	DR	JS	BL	f2	s5	a	a	c
Euterpe oleracea Martius	2.33	30.28	13.70		TT	DR	FK	BL	f1	s5	a	d	c

Species													
Geonoma cf. *deversa* (Poiteau) Kunth				0.07	SA	DR	JS	BL	f1	s4	a	b	b
Geonoma stricta (Poiteau) Kunth	1.35	1.19	1.14	0.32	SA	DR	JS	BU	f1	s4	a	a	c
Oenocarpus bacaba Martius			2.25		TT	DR	FK	BL	f1	s5	a	d	c
Bombacaceae													
Quararibea duckei Hubert				0.42	ST	DR	FT	BR	f2	s2	a	b	b
Boraginaceae													
Cordia sp 1				0.10	MT	PO	JS	GR	f3	s5	a	d	b
Burseraceae													
Protium cf. *neglectum* Swart	0.04		0.46	0.35	TT	CA	JS	WH	f4	s4	a	d	b
Protium subserratum (Engler) Engler	0.01				TT	CA	JS	WH	f3	s4	a	d	b
Tetragastris altissima (Aublet) Martius	0.04		0.36		TT	CA	JS	WH	f3	s4	a	d	b
Tetragastris sp 1		2.14			TT	CA	JS	WH	f3	s4	a	d	b
Trattinickia sp 1			5.03		TT	DR	JS	BL	f1	s5	a	d	a
Cecropiaceae													
Cecropia obtusa Trecul	0.01				MT	BE	FT	GR	f1	s3	d	c	b
Cecropia sciadophylla Martius	0.01				TT	BE	JS	BR	f1	s3	d	c	b
Coussapoa latifolia Aublet	1.76	0.74	0.83	0.07	EP	BE	JS	YE	f1	s4	c	d	c
Coussapoa microcephala Trecul	0.01	2.26	0.10		EP	BE	JS	YE	f1	s4	c	d	c
Pourouma sp 1	0.55				TT	DR	JS	BL	f2	s4	a	d	b
Celastraceae													
Goupia glabra Aublet	5.84				TT	BE	JS	RE	f1	s3	a	d	b
Chrysobalanaceae													
Licania cf. laxiflora Fritsch				5.87	TT	DR	FK	BR	f1	s4	a	c	b
Licania sp 1	0.04			4.83	TT	DR	JS	BR	f2	s5	a	c	b
Clusiaceae													
Symphonia globulifera Linnaeus				1.28	TT	DR	JS	GR	f1	s1	a	d	c
Connaraceae													
Connarus sp 1		0.72			LI	CA	FT	YE	f3	s2	a	d	b
Cucurbitaceae													
Cayaponia ophtalmica R.E. Schultes	0.01			12.28	LI	PO	FT	WH	f2	s3	a	b	b
Cayaponia sp 1			9.62		LI	PO	FT	WH	f2	s3	a	b	b
Euphorbiaceae													

Species												
Drypetes fanshawei Sandwith	0.93				MT	DR	JS	GR	f1	s4	a	c	b
Drypetes variabilis Uittien	0.16				TT	DR	JS	YE	f1	s5	a	d	c
Hyeronima laxiflora (Tulasne) Mueller-Argoviensis	0.01		0.14	0.05	TT	DR	FK	RE	f1	s5	a	d	b
Margaritaria nobilis Linnaeus			4.07		MT	CA	FT	BU	f2	s2	b	d	b
Flacourtiaceae													
Laetia procera (Poeppig) Eichler			0.01		TT	CA	JS	WH	f2	s3	c	d	c
Hippocrateaceae													
Cheiloglinum sp 1		4.22			LI	PO	JS	YE	f3	s3	b	b	b
Humiriaceae													
Humiria balsamifera (Aublet) Saint-Hilaire			0.22	0.21	TT	DR	JS	BL	f1	s4	a	d	a
Sacoglottis cydonioides Martius	1.60				TT	DR	FK	RE	f1	s5	a	d	b
Sacoglottis guianensis Bentham	0.01	0.13			TT	DR	JS	YE	f1	s5	a	d	b
Icacinaceae													
Poraqueiba guianensis Aublet	1.71				MT	DR	FK	GR	f1	s3	a	c	b
Lauraceae													
Nectandra globosa (Aubl.) Mez				0.10	MT	DR	JS	GR	f1	s2	a	d	a
Ocotea sp 1	4.50		31.95		TT	DR	JS	BL	f1	s2	a	d	b
Ocotea floribunda (Sw.) Mez	0.37			1.32	TT	DR	JS	BL	f1	s2	a	d	b
Liliaceae													
Smilax sp 1	0.01		0.14		LI	DR	JS	RE	f1	s4	a	c	b
Malpighiaceae													
Byrsonima sp 1			2.43		MT	DR	JS	YE	f2	s4	a	d	a
Marantaceae													
Calathea cf. *elliptica* (Roscoe) K. Schumann	0.03				SA	CA	FT	BU	f3	s4	b	b	c
Marcgraviaceae													
Marcgravia cf. *coriacea* Vahl			0.07		LI	CA	FT	RE	f2	s1	d	c	b
Marcgravia sp 1			0.31		LI	CA	FT	RE	f2	s1	d	c	b
Melastomataceae													
Miconia sp 1			0.11		ST	BE	JS	BU	f1	s4	b	d	b
Meliaceae													
Guarea gomma Pulle	6.04		0.84	5.77	TT	CA	FT	RE	f3	s4	b	d	b
Guarea grandifolia A.P. De Candolle	12.42		1.69		TT	CA	FT	RE	f4	s4	b	c	a

Species													
Guarea kunthiana Adr. Jussieu	10.99		1.50		TT	CA	FT	RE	f4	s4	b	c	b
Trichilia septentrionalis C. De Candolle	0.01		2.15		MT	CA	FT	RE	f3	s2	a	c	b
Menispermaceae													
Abuta cf. *grandifolia*	0.61				SA	PO	JS	YE	f3	s4	a	b	b
Abuta sp.	1.63				LI	PO	JS	YE	f3	s4	a	b	b
Orthomene sp 1	1.14	0.20			LI	PO	JS	YE	f3	s4	a	c	a
Mimosaceae													
Abarema curvicarpa (H.S. Irwin) Barneby & J.W. Grimes			0.08		MT	CA	FT	BU	f4	s1	b	d	b
Abarema jupunba (Willd.) Britton & Killip			0.06		TT	CA	FT	BU	f4	s1	b	d	a
Balizia pedicellaris (DC.) Barneby & J.W. Grimes			0.43		TT	CA	FT	BU	f4	s3	c	d	b
Inga sp 1	2.33	1.95			MT	PO	JS	YE	f3	s1	b	d	b
Parkia cf. *ulei* (Harms) Kuhlmann	0.01				TT	CA	FT	BL	f4	s4	c	d	b
Moraceae													
Brosimum parinarioides Ducke	2.98	2.23			TT	DR	FK	GR	f1	s2	a	d	b
Brosimum rubescens Taubert	0.08				TT	DR	JS	YE	f1	s2	a	d	b
Ficus cf. *leiophylla* C.C. Berg			0.78		EP	BE	JS	YE	f1	s3	c	d	b
Heliocostylis cf. *tomentosa* (Poeppig & Endlicher) Rusby			0.48		TT	BE	JS	YE	f1	s3	b	d	b
Naucleopsis guianensis (Mildbraed) C.C. Berg	0.40				MT	PO	FT	WH	f3	s3	b	c	b
Myristicaceae													
Iryanthera sagotiana (Bentham) Warburg	0.01				MT	CA	FT	RE	f3	s4	a	d	c
Virola michelii Heckel	0.02			5.24	TT	CA	FT	RE	f3	s4	a	d	c
Virola multicostata Ducke				2.32	MT	CA	FT	RE	f3	s4	a	d	a
Virola sebifera Aublet				6.79	TT	CA	FT	RE	f3	s4	a	d	a
Virola kwatae Sabatier				5.00	TT	CA	FT	RE	f3	s4	a	d	b
Virola surinamensis (Rolander) Warburg				25.34	TT	CA	FT	RE	f3	s4	a	d	b
Myrsinaceae													
Ardisia guianensis (Aublet) Mez & Chase			0.06		SA	DR	FT	BL	f1	s3	a	b	a
Ardisia sp 1			0.06		SA	DR	FT	BL	f1	s3	a	b	a
Myrtaceae													
Eugenia coffeifolia De Candolle	15.55	34.80	10.70	2.14	ST	DR	JS	BL	f1	s5	a	d	b
Eugenia patrisii Vahl			0.36		MT	DR	JS	RE	f1	s3	a	c	b

Species													
Stylogyne sp 1			0.29		SA	DR	FT	RE	f1	s3	a	b	a
Olacaceae													
Minquartia guianensis Aublet	0.01	9.02			TT	DR	JS	BL	f1	s5	a	d	b
Papilionaceae													
Dussia discolor Amshoff	3.19				TT	CA	JS	RE	f3	s1	a	d	a
Polygonaceae													
Coccoloba sp 1			0.26		LI	DR	JS	BL	f1	s4	a	c	b
Rhamnaceae													
Ziziphus cinnamomum Triana & Planch	2.78	1.30			TT	PO	JS	YE	f3	s4	a	d	a
Rubiaceae													
Faramea guianensis (Aublet) Bremekamp			0.01	0.06	SA	DR	JS	BL	f1	s4	a	a	b
Faramea lourteigiana Steyermark			0.15		SA	DR	JS	BU	f1	s4	a	a	c
Guettarda acreana Krause		0.63	0.07		MT	DR	JS	BL	f1	s3	a	c	a
Psychotria bahiensis A. De Candolle	0.08	0.04		0.02	SA	BE	JS	WH	f1	s4	a	b	b
Psychotria ficigemma DC.	0.01		0.83	0.21	SA	BE	JS	RE	f1	s4	a	b	b
Psychotria kappleri (Miquel) Mueller-Argoviensis	0.08	0.05	0.13		SA	BE	JS	BU	f1	s4	a	a	c
Psychotria moroidea Steyermark	0.01				SA	BE	JS	RE	f1	s4	a	b	c
Psychotria oblonga (De Candolle) Steyermark	1.33	0.05	0.09	0.19	SA	BE	JS	WH	f1	s4	a	b	c
Psychotria sp 1	0.01		0.09		SA	BE	JS	BU	f1	s4	a	b	b
Sapindaceae													
Cupania scrobiculata L.C. Richard	0.31				ST	CA	FT	YE	f3	s3	b	c	c
Cupania sp 1	0.01				ST	CA	FT	YE	f3	s3	b	c	c
Paullinia alata (Ruiz & Pavon) G. Don			0.35		LI	CA	FT	WH	f3	s3	a	c	a
Paullinia plagioptera Radlkofer			4.92		LI	CA	FT	WH	f3	s3	a	c	a
Sapotaceae													
Pouteria cf. *bilocularis* (Winckler) Baehni	2.47				MT	PO	JS	YE	f3	s4	a	c	b
Vitaceae													
Cissus sp 1		0.02			LI	BE	JS	BL	f1	s4	a	c	a
Zingiberaceae													
Renealmia guianensis Maas			0.70		SA	CA	FT	YE	f2	s4	c	c	b
Renealmia sp 1			0.65		SA	CA	FT	YE	f2	s4	c	c	b
Σ	100.00	100.00	100.00	100.00									

Frequency distribution of the plant species, according to their biological abundance and fruit characteristics, in the diets of the four large frugivorous bird species.

Bird species	Crax n=60	Penelope n=20	Psophia n=45	Tinamus n=35	Σ n=105
Number of plant species					
Plant biological type					
sapling	11	4	12	7	19
small tree	7	1	3	6	10
middle tree	9	2	5	4	17
epiphyte	3	2	3	1	4
liana	4	4	7	2	14
tall tree	26	7	15	15	41
Fruit type					
berry	12	6	9	4	16
drupe	24	8	18	19	42
capsule	15	2	15	10	33
pod	8	4	1	2	11
dry	1	0	2	0	3
Type of edible tissue					
juicy soft	39	17	23	21	59
fleshy thin	14	1	16	11	35
fleshy thick	6	2	4	3	8
pulpless	1	0	2	0	3
Fruit colour					
green	5	1	0	3	8
brown	3	0	2	5	8
yellow	13	8	7	1	20
black	12	6	10	9	22
white	9	3	8	4	15
blue	4	2	6	4	10
red	14	0	11	9	22
Fruit protection					
soft	28	13	26	16	47
easy	10	1	9	8	21
difficult	18	6	5	7	28
very difficult	3	0	5	4	9
Seed protection					
soft	3	1	3	3	9
easy	6	2	4	3	11
difficult	8	2	11	2	21
very difficult	33	11	21	21	51
very hard	10	4	6	6	13

Number of seeds

1-2	45	16	29	29	74
3-10	10	2	8	3	18
11-100	3	2	6	3	9
> 100	2	0	2	0	4

Fruit production

< 1	4	2	4	5	7
10-100	12	3	9	7	20
100-1 000	16	3	13	4	28
> 1 000	28	12	19	19	50

Species abundance

Rare	6	4	10	5	20
Frequent	37	10	24	24	63
Abundant	17	6	11	6	22

APPENDIX 3

Distribution of biological, abundance, and fruit characteristics in the fruit diet of each large frugivorous bird species

%N = percentage of the number of plant species with character-state i in the diet of bird species j.

%Q = percentage of weight of drained fruits with character-state i in the diet of bird species j.

Bird species	Crax		Penelope		Psophia		Tinamus		Seed Predators		Seed Dispersers	
Plant variables	% N	% Q	% N	% Q	% N	% Q	% N	% Q	% N	% Q	% N	% Q
Plant biological type												
Sapling	18.33	3.55	20.00	1.33	26.66	4.17	20.00	7.52	19	5	23	3
Small tree	11.67	26.70	5.00	34.81	6.67	10.88	17.14	5.84	15	16	6	23
Middle tree	15.00	10.78	10.00	2.58	11.11	9.04	11.43	2.60	13	7	11	6
Epiphyte	5.00	1.78	10.00	3.00	6.67	1.70	2.86	0.07	4	1	8	2
Liana	6.67	2.79	20.00	5.16	15.56	15.58	5.71	12.54	6	8	18	10
Tall tree	43.33	54.40	35.00	53.12	33.33	58.63	42.86	71.43	43	63	34	56
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100
Fruit type												
Berry	20.34	9.16	30.00	3.16	20.93	3.42	11.43	0.49	16	5	25.5	3
Drupe	40.68	46.33	40.00	86.31	41.86	68.82	54.29	35.75	47	41	41	77.5
Capsule	25.42	33.15	10.00	2.86	34.88	18.14	28.57	51.38	27	42	22.5	10.5
Pod	13.56	11.36	20.00	7.67	2.33	9.62	5.71	12.38	10	12	11	9
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100
Type of edible tissue												
Juicy soft	66.1	54.00	85.00	66.78	53.49	56.44	60.00	29.86	63	42	69	62
Fleshy thin	23.73	30.29	5.00	0.72	37.21	27.34	31.43	63.73	28	47	21	11
Fleshy thick	10.17	15.71	10.00	32.50	9.30	16.22	8.57	6.41	9	11	10	27
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100

Fruit colour

Green	8.33	5.65	5.00	2.23	0.00	0.00	8.57	1.48	8.5	4	2.5	1.5
Brown	5.00	3.65	0.00	0.00	4.44	0.46	14.29	11.49	10	8	2	0.5
Yellow	21.67	13.30	40.00	11.52	15.56	5.95	2.86	0.07	12	7	28	9
Black	20.00	26.78	30.00	82.78	22.22	63.73	25.71	22.02	23	24	26	73
White	15.00	1.93	15.00	2.23	17.78	15.77	11.43	12.84	13	7	16	9
Blue	6.67	1.47	10.00	1.24	13.33	5.65	11.43	0.89	9	1	12	3
Red	23.33	47.22	0.00	0.00	26.67	8.44	25.71	51.21	24.5	49	13.5	4
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100

Fruit protection

f1	46.66	47.82	65.00	81.44	57.78	69.48	45.71	12.66	46	30.5	61.5	75.5
f2	16.67	7.67	5.00	8.03	20.00	17.82	22.86	35.86	20	22	12.5	13
f3	30.00	21.05	30.00	10.53	11.11	8.59	20.00	50.56	25	35.5	20	10
f4	6.67	23.46	0.00	0.00	11.11	4.11	11.43	0.92	9	12	6	1.5
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100

Seed protection

s1	5.00	5.54	5.00	1.95	6.67	0.61	8.57	1.42	7	3.5	6	1.5
s2	10.00	7.95	10.00	2.95	8.89	38.21	8.57	1.84	9	5	9.5	20.5
s3	13.33	8.29	10.00	4.85	24.44	16.93	5.71	12.71	9.5	10.5	17	11
s4	55.00	51.42	55.00	16.02	46.67	12.46	60.00	69.77	57.5	60.5	51	14
s5	16.67	26.80	20.00	74.23	13.33	31.79	17.15	14.26	17	20.5	16.5	53
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100

Number of seeds

1-2s	75.00	65.65	80.00	90.83	64.45	87.63	82.86	93.29	79	80	72	89
3-10s	16.67	32.55	10.00	6.17	17.78	8.93	8.57	5.91	13	19	14	7.5
11-100s	5.00	1.78	10.00	3.00	13.33	3.06	8.57	0.80	7	1	12	3
> 100s	3.33	0.02	0.00	0.00	4.44	0.38	0.00	0.00	1	ε	2	0.5
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100

Fruit production

< 10f	6.67	5.05	10.00	1.24	8.89	1.42	14.29	7.40	10.5	6	9.5	1
10-100f	20.00	13.73	15.00	4.31	20.00	11.34	20.00	13.68	20	14	17.5	8
100-1 000f	26.67	30.61	15.00	0.85	28.89	13.11	11.43	13.38	19	22	22	7
> 1 000f	46.66	50.61	60.00	93.60	42.22	74.13	54.28	65.54	50.5	58	51	84
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100

Species abundance

Rare	10.00	22.45	20.00	2.15	22.22	15.07	14.29	9.48	12	16	21	8.5
Frequent	61.67	62.89	50.00	63.29	53.34	66.27	68.57	76.35	65	69.5	52	65
Abundant	28.33	14.66	30.00	34.56	24.44	18.66	17.14	14.17	23	14.5	27	26.5
Σ	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100	100	100	100