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EFFECT OF FRUIT SIZE ON PRIMARY SEED DISPERSAL OF FIVE CANOPY TREE SPECIES OF THE COLOMBIAN AMAZON

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ABSTRACT. Primary seed dispersal at the canopy level was recorded by the authors in 1996 in five tree species of a terra firme forest along the Caquetá River in the Colombian Amazon. The trees were *Trattinnickia* sp. (Burseraceae), *Hebepetalum humiriifolium* and *Roucheria columbiana* (Linaceae), *Ocotea* sp. (Lauraceae), and *Micropholis venulosa* (Sapotaceae). With these single-seeded species, we tested the hypothesis that the larger the fruit size, the lower the amount of seeds dispersed. We also evaluated the effect of fruit size and other fruit characteristics such as seed size, fruit mass, and percentage of pulp on the feeding behavior of diurnal frugivores (such as feeding rates, fruit removal, fruit damage). Primary seed dispersal was calculated as the difference between the number of fruits taken by birds or mammals minus seeds dropped, regurgitated, defecated, and damaged at the tree after removal. Seed dispersal also was estimated by counting the number and frequency of frugivore species at the tree and the percentage of fruits taken by animals relative to the fruit crop size. Results showed that primary seed dispersal was lower for larger fruits only when calculated as the seeds carried away from the tree crown by frugivores. This relationship did not hold when primary seed dispersal was estimated by counting the number and frequency of visitors (species) and the percentage of fruits taken. Fruit size affected seed dispersal more than did seed size, fruit mass, or pulp content. In addition, larger fruit size was negatively correlated with the number of visits and positively correlated with fruit-handling times. Among the 33 bird species observed during the study, only *Trogon melanurus, T. violaceus, Ramphastos tucanus,* and *Querula purpurata* can be considered major seed dispersers for the five tree species. The primates, (*Saguinus fuscicollis, Callicebus torquatus*) were not major seed dispersers for the five tree species studied.

RESUMEN. Se registró la dispersión primaria de semillas en cinco especies de árboles del dosel de un bosque de Tierra Firme del Río Caquetá, Amazonía colombiana en 1996. Los árboles estudiados fueron *Trattinnickia* sp. (Burseraceae), *Hebepetalum humiriifolium* y *Roucheria columbiana* (Linaceae), *Ocotea* sp. (Lauraceae), y *Micropholis venulosa* (Sapotaceae). Con estas especies, de frutos de una sola semilla, se probó la hipótesis que a mayor tamaño del fruto menor dispersión de semillas. También se evaluó el efecto del tamaño del fruto y otras características del fruto como el tamaño de la semilla, el peso del fruto y el porcentaje de pulpa, en los comportamientos alimenticios de los frugívoros (como tasas de alimentación, daño y tiempo de manipulación de los frutos). La dispersión primaria de semillas se calculó al descontar de los frutos tomados por aves o mamíferos las semillas botadas, regurgitadas, defecadas, y dañadas en el árbol después de haber sido removidas. La dispersión de semillas también se estimó por medio del número y la frecuencia de frugívoros en el árbol y por el porcentaje de frutos removidos por animales respecto al tamaño de la cosecha. Los resultados mostraron que la dispersión primaria de semillas calculada como las semillas alejadas de la copa del parental por frugívoros, fue menor para los frutos de mayor tamaño. No se presentó esta relación cuando la dispersión primaria se estimó como el número, la frecuencia de visitantes (especies) o como el porcentaje de frutos removidos. La relación entre el tamaño del fruto y la dispersión de semillas fue significativamente positiva, a diferencia de las correlaciones de la dispersión con el tamaño de la semilla, el peso del fruto y la cantidad de pulpa. Se encontró que a mayor tamaño del fruto menor numero de visitas y mayor tiempo de manipulación del fruto. De las 33 especies de aves observadas durante este estudio *Trogon melanurus, T. violaceus, Ramphastos tucanus,* y *Querula purpurata* pueden considerarse grandes dispersores de semillas de estas cinco especies de árboles. Los primates (*Saguinus fuscicollis, Callicebus torquatus*) no fueron importantes dispersores de dichas especies.

Key words: frugivory, seed dispersal, canopy, Colombian Amazon, fruit size, feeding behavior

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Introduction

Physical and chemical characteristics of fruits and seeds, as well as frugivore morphology, physiology, and behavior, have been considered critical factors that affect seed dispersal. Fruit characteristics that generate variations in both the quantity and the quality of dispersal, which affect accessibility and selection by frugivores, are fruit and seed size, nutritional content and chemical composition of fruits and seeds, color, texture and thickness of fruit coat, fruit and seed mass, number of seeds per fruit, and amount of pulp (McKey 1975, Howe 1982, Howe & Smallwood 1982, Janson 1983, Pratt & Stiles 1983, Wheelwright 1985, 1993, Herrera 1986, Levey 1986, 1987, Moermond et al. 1986, Fleming et al. 1993, Martinez del Rio & Restrepo 1993, Murray et al. 1993). Plant characteristics, such as fruiting patterns and fruit crop size, also have been suggested as limiting dispersal factors (Howe 1982, Wheelwright 1985, Herrera 1986, Murray 1987, Jordano & Schupp 2000).

Some authors propose that efficient seed dispersal performed by a given frugivore depends on both quantity and quality components of the animal's behavior (Schupp 1993, Jordano & Schupp 2000). High quantity and quality components of frugivore behavior can be measured by the avoidance of seed damage, by the removal of seeds from the vicinity of the parent tree, by a high frequency of visits, high feeding rates during short fruit-handling times, and by deliverance of unharmed seeds to habitats suitable for germination and growth (McKey 1975, Howe 1982, 1990, Howe & Smallwood 1982, Pratt & Stiles 1983, Moermond & Denslow 1985, Herrera 1986, Levey 1986, 1987, Murray 1987, Martinez del Rio & Restrepo 1993, Schupp 1993, Wheelwright 1993, Jordano & Schupp 2000).

Our study analyzed the effect of some fruit characteristics (i.e., fruit size, fruit mass, seed size, and percentage of pulp) on primary seed dispersal of five canopy tree species of a terra firme forest in the Colombian Amazon. Primary seed dispersal is defined here as the transport of viable seeds away from the parent tree. Quality components of dispersal effectiveness (sensu Jordano & Schupp 2000), thus were not assessed because of the difficulty in establishing the fate of seeds after their removal or ingestion by animals. During such times, factors such as secondary seed dispersal, predation, competition, site condition, allelopathy, and gap dynamics may influence seed and seedling survival (Nathan & Muller-Landau 2000, Bleher & Böhning-Gaese 2001). Additionally, we studied the effect of fruit characteristics on feeding behavior of diurnal frugivores (e.g., feeding rates, fruits dropped, and fruit-handling times). With changes in a fruit characteristic that affects the feeding behavior of animals, we expected to observe significant differences of feeding rates, fruit-handling times, and seeds dropped and carried away.

Materials and Methods

Study Site and Plant Species

The research was conducted at the biological station of the Tropenbos-Colombia Foundation, located in the indigenous community Nonuya of Peña Roja (0°39′S, 72°06′W) in the Middle Caquetá River region, Departamento del Amazonas, Colombia. According to Holdridge et al. (1971), this region is classified as Humid Tropical Forest. The study site is a terra firme forest on the High Terraces of the Caquetá River (Duivenvoorden & Lips 1993). Mean annual temperature is 25.7°C and rainfall averages 3059 mm per year. Although the area does not have a marked dry season (months with less than 100 mm), rainfall decreases between December and February, while the highest levels occur in May and June.

From March to July 1996, frugivore visits and fruit removal were recorded in five canopy tree species with fleshy and single-seeded fruits having a thin coat, but otherwise fruit size differed among them. Studied species were *Trattinnickia* sp. (Burseraceae), *Hebepetalum humiriifolium* (Planch.) Benth. and *Roucheria columbiana* Hallier f. (Linaceae), *Ocotea* sp. (Lauraceae), and *Micropholis venulosa* Pierre (Sapotaceae). As the tree species were located in a 110 m x 40 m plot, only one individual per species was studied. Fruits of every tree were characterized by measuring, weighing, and describing a sample of 50 fruits. Fruit and seed length was measured with calipers to the nearest 0.01 mm. Average of fruit and seed length was used to describe fruit and seed size, respectively. Percentage of pulp was estimated as the difference between fruit and seed size. Pulp type was described as soft, hard, juicy, or oily. Vouchers of every species were collected and determined at the Colombian Amazonic Herbarium (COAH).

Frugivore Observations

Observations were made from an aerial walkway 50 m long and 27 m high, using binoculars (7× 35 mm and 8× 40 mm) and a telescope (20–60×–60 mm). When observations were not possible from the walkway, we made recordings from a nearby tree accessed by single rope techniques. A total of 195 hours of observation were

TABLE 1. Fruit characteristics of the five tree species studied in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996. Pulp types are soft, firm, juicy, or oily. Mean and standard deviations are based on measurements of 50 fruits and seeds per plant.

Tree species	Fruit size (cm)	Seed size (cm)	Fruit mass (g)	% of pulp	Pulp type
Trattinnickia sp.	1.514 ± 0.120	0.719 ± 0.058	0.586 ± 0.103	52.51	soft, juicy
Ocotea sp.	1.343 ± 0.066	0.838 ± 0.039	1.174 ± 0.117	37.62	firm, oily
Hebepetalum humiriifolium	0.738 ± 0.060	0.578 ± 0.059	1.314 ± 0.298	60.19	soft, juicy
Roucheria columbiana	1.243 ± 0.067	0.496 ± 0.041	0.379 ± 0.046	21.64	soft, juicy
Micropholis venulosa	1.517 ± 0.085	0.829 ± 0.065	1.880 ± 0.465	52.49	firm, juicy
F (one-way ANOVA)	751.34 ($P < 0.05$)	405.17 ($P < 0.05$)	271.60 ($P < 0.05$)	363.90 ($P < 0.05$)	

recorded at different time intervals between 0600 to 1800 hours. Each tree was observed for a total of 36–42 hours, 5 hours per day, alternating trees among days. No recordings were made during rainy days. By conducting scan sampling (Martin & Bateson 1986) of the tree crown every 15 minutes, we recorded animal species and number of individuals per species. Animals were included in the analysis only if they fed on fruits. Birds were classified as legitimate frugivores or predators (Snow 1981, Wheelwright et al. 1984, Moermond & Denslow 1985). Focal sampling (Martin & Bateson 1986) was used to record time of arrival and departure of frugivores (visit length) and their feeding behavior, such as number of fruits removed, dropped, and damaged during a visit. Feeding rates (number of fruits taken per feeding visit), fruit handling times before ingestion, and activities such as regurgitation, defecation, and interaction with other animals also were recorded. Repeat visits by the same animal were treated in the same manner as visits by different animals.

Seed Dispersal

Primary seed dispersal was estimated in terms of the number of animal species at the tree crown, the frequency of animal visitation, the percentage of the fruit crop taken, and the percentage of seeds carried away from the parent tree relative to the fruits taken by frugivores. The first three of these primary seed dispersal estimators have been used in several studies (e.g., McKey 1975, Howe 1982, 1990, Janson 1983, Wheelwright 1985, 1993, Levey 1986, Murray 1987). The fourth estimator was calculated, for each tree species, as the number of seeds leaving the tree through the activity of frugivore animals, relative to the total number of fruits taken by diurnal frugivores. The number of seeds leaving the tree was calculated as the difference between the number of fruits taken by animals and the seeds dropped and damaged before being swallowed. Regurgitated seeds and those swallowed when the animal defecated on the tree after visits longer than 15 minutes also were discounted (Levey 1986). Seeds carried away by seed predators were considered as nondispersed (Snow 1981, Wheelwright et al. 1984).

Data Analysis

To evaluate whether or not fruit characteristics are significantly different between tree species, we made one-way ANOVA analyses and the Tukey multiple comparison test (Zar 1984). On the other hand, to determine the rate of fruit crop reduction for the five tree species, we counted the number of fruits on the same branches every day and multiplied it by the total number of branches estimated for each tree (Murray 1987). The slope of the linear regression between time and number of fruits counted per day was considered as the rate of fruit crop reduction. This

TABLE 2. Fruit crop reduction and fruit removal by diurnal frugivores in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996.

Tree species	Fruit crop reduction (No. fruits/day)	Fruit removal by diurnal frugivores	
		(No. fruits/day)	%
Trattinnickia sp.	1312	337	25.8
Ocotea sp.	345	43	12.4
Hebepetalum humirifolium	1089	335	30.8
Roucheria punctata	902	109	12.1
Micropholis venulosa	760	119	15.7

TABLE 3. Primary seed dispersal of the five tree species studied in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996. Primary seed dispersal in terms of the percentage of seeds carried away from the parent tree relative to the fruits taken by diurnal frugivores, the number of animal species (frugivores) at the tree crown, the frequency of animal visitation, and the percentage of fruits taken relative to fruit crop size.

Tree species	Seeds carried away (%)	No. of frugivores	Frequecy of animal visitation (No. observations/ hour)	Fruits taken (%)
Trattinnickia sp.	20.73	21	2.95	12.57
Ocotea sp.	57.89	16	1.4	3.74
Hebepetalum humiriifolium	67.51	21	5.58	12.97
Roucheria columbiana	72.7	14	3.71	4.9
Micropholis venulosa	33.98	14	1.61	3.64

rate, which is influenced by multiple factors such as rain, wind, and diurnal and nocturnal fruit removal by frugivores, was compared with the rate of fruit removal by diurnal frugivores. The latter was calculated as the mean of the fruits taken between 0600 and 1800 hours.

Correlations (Pearson's product moment correlation and Spearman's rank correlation) between the different estimators of primary seed dispersal were used to identify the best indicator of seed dispersal. We also used correlations to determine the effect of fruit size, fruit mass, seed size, and percentage of pulp on primary seed dispersal. To analyze primary seed dispersal differences between tree species and to see if such differences were consistent with the results obtained with correlations of a single fruit characteristic, we used one way ANOVAs and the Tukey multiple comparison test with tree species as the main effect and seeds carried away as a dependent variable.

To evaluate which fruit-eating animals perform high quality primary seed dispersal, we selected those that visited at least four of the five tree species studied. Only animals with more than two recordings at the tree were considered. For these animals, we estimated their "potential" contribution to seed dispersal by multiplying the proportion of seeds carried away per animal species and the mean number of individuals per species at the tree (obtained by the scan sampling). To estimate the effect of fruit characteristics on animal behavior, we also used correlations, one way ANOVAs, and the Tukey multiple comparison test. To minimize the influence of possible feeding rate variation, we excluded from the analysis fruits taken during interactions with individuals of the same or different species and fruits taken in the afternoon hours (Howe 1982).

RESULTS

Fruit Characteristics

Fruit size, seed size, fruit mass, and percentage of pulp differed significantly among the five tree species studied (TABLE 1). The Tukey multiple comparison test, however, showed that fruit size differences between *Trattinnickia* sp. and *Micropholis venulosa* were not significant (Tukey multiple comparison test $q_{245,5} = 0.313$, $P >$

TABLE 4. Correlation matrix of primary seed dispersal estimators of the five tree species studied in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996. * Pearson product moment correlation (r). ** Spearman rank correlation (r_s). Boldface figures, $P < 0.05$.

Estimators of primary seed dispersal	No. of frugivores	Fruits taken‡ (%)	Frequency of animal visitation (No. observations/hour)
Seeds carried away †(%)	0.0513**	−0.186*	0.475*
P	0.437	0.352	0.180
No. of frugivores		**0.949****	**0.791****
P		0.007	0.050
Fruits taken ‡ (%)			0.713*
P			0.055

† Percent of seeds carried away from the parent tree relative to the fruits taken by diurnal frugivores.
‡ Percent of fruits taken by diurnal frugivores relative to the fruit crop size.

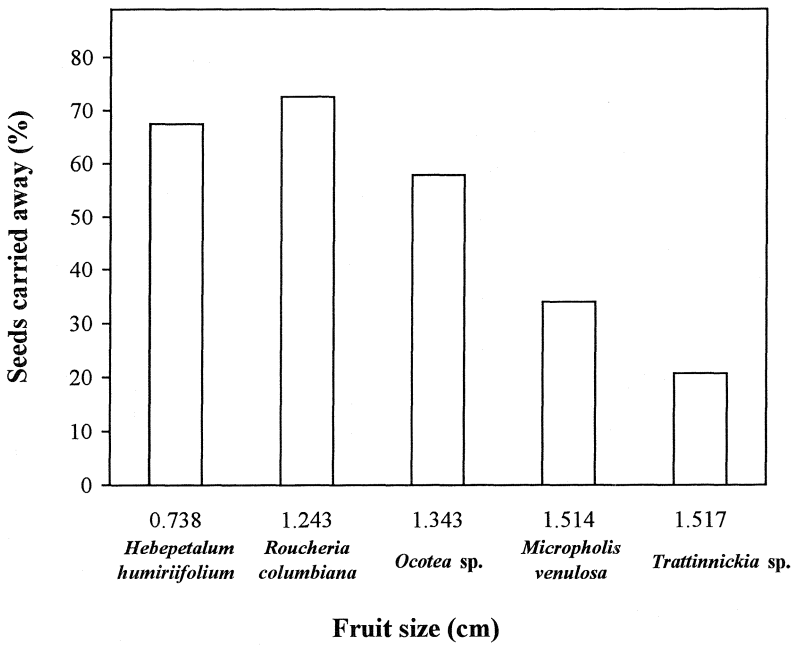

FIGURE 1. Percentage of seeds carried away from the parent tree relative to the fruits taken by frugivores, as a function of fruit size (Pearson product-moment correlation coefficient $r = 0.718$, $P < 0.05$) in a terra firme forest site along the Caqueta River, Amazonas Colombia, 1996.

0.05). Seed size differences were not significant between *Ocotea* sp. and *Micropholis venulosa* ($q_{245,5} = 1.169$ $P > 0.05$), neither were differences in percentage of pulp between *Trattinnickia* sp. and *Ocotea* sp. ($q_{245,5} = 0.014$ $P > 0.05$).

Reduction of Fruit Crop and Fruit Removal

During the observation period, the total fruit crop reduction rate differed among species (TABLE 2). *Trattinnickia* sp. showed the highest rate (1312 fruits/day), and *Ocotea* sp. showed the lowest rate (346 fruits/day). For each tree, rates of fruit removal by diurnal frugivores were significantly lower than the rate of fruit crop reduction, since the latter also includes factors such as rain, wind, and removal by evening and nocturnal animals. The highest rate of fruit removal by diurnal frugivores was recorded for *Trattinnickia* sp. (337 fruits/day) and the lowest for *Ocotea* sp. (43 fruits/day). Rates of fruit re-

TABLE 5. Correlation matrix of primary seed dispersal estimators and fruit characteristics of the five tree species studied in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996. * Pearson product moment correlation (r), ** Spearman rank correlation (r_s). Boldface figures, $P < 0.05$.

Estimators of primary seed dispersal	Fruit characteristics			
	Fruit size (cm)	Seed size (cm)	Fruit mass (g)	% of pulp
Seeds carried away (%)	**−0.718***	−0.610*	−0.085*	−0.337*
P	0.050	0.107	0.416	0.260
No. of frugivores	−0.158**	−0.632**	−0.701**	−0.360**
P	0.400	0.126	0.060	0.276
Fruits taken (%)	−0.458*	−0.362*	**−0.906***	−0.444*
P	0.199	0.244	0.017	0.197
Frequency of animal visitation (No. observations/hour)	**−0.853***	**−0.828***	−0.703*	−0.462*
P	0.033	0.040	0.073	0.197

TABLE 6. Frugivores visiting, more than two times, at least four of the five tree species studied in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996. Frugivore contribution to tree primary seed dispersal calculated as the percentage of seeds primarily dispersed multiplied by the mean number of individuals per species visiting the tree.

	Hebepetalum humiriifolium			*Roucheria columbiana*		
Frugivore species	*N*	No. individuals per visit	Frugivore contribution (% seeds carried away)	*N*	No. individuals per visit	Frugivore contribution (% seeds carried away)
Trogon melanurus	10	1.20	2.04	5	1.10	3.04
Trogon violaceus	5	1.50	1.22	5	1.20	2.94
Ramphastos tucanus	24	1.30	19.11	2	1.00	19.63
Phoenicircus nigricollis	20	1.07	12.47	18	1.00	8.59
Querula purpurata	13	1.80	4.65	6	1.60	3.44
Turdus ignobilis debilis	27	1.20	6.38	30	1.20	18.77
Turdus obsoletus	10	1.03	2.66	28	1.10	8.10

moval by diurnal frugivores of the five tree species ranged between 12.4% and 30.8% of fruit crop reduction.

Primary Seed Dispersal

The highest percentage of seeds carried away relative to the fruits taken by frugivores was measured for *Roucheria columbiana* (72.70%), and the lowest for *Trattinnickia* sp. (20.73%) (TABLE 3). Seeds dropped under the tree crown or damaged by frugivores were considered as non-dispersed; they ranged from 27.36% in *R. columbiana* to 79.1% in *Trattinnickia* sp. Only seeds of trees with the largest fruit sizes were damaged at the canopy level by frugivores *(Micropholis venulosa* 10.1%, *Trattinnickia* sp. 15.9%).

The number of animal species visiting individual trees ranged from 13 species at *Micropholis venulosa* to 21 species at *Hebepetalum humiriifolium* and *Trattinnickia* sp. (TABLE 3). *Hebepetalum humiriifolium* showed the highest frequency of animal visitation (5.6 observations/hour), and *Ocotea* sp. the lowest (1.4 observations/hour). Additionally, the highest percentage of fruits taken relative to the fruit crop size was obtained in *H. humiriifolium* and in *Trattinnickia* sp. (12.57% and 12.97%, respectively), while the lowest occurred in *M. venulosa* (3.64%). Correlations of these seed dispersal estimators and the percentage of seeds carried away were not statistically significant ($P > 0.05$) (TABLE 4). The number of frugivores, however, was positively correlated with the percentage of fruits taken relative to the fruit crop (Spearman rank correlation $r_s = 0.949$, $P < 0.05$) and with the frequency of animal visitation ($r_s = 0.791$, $P < 0.05$).

A significant negative correlation was found between fruit size and the percentage of seeds carried away from the parent tree (Pearson product-moment correlation $r = -0.718$, $P < 0.05$) (FIGURE 1). This percentage was not correlated with fruit mass, seed size, and pulp content ($P > 0.05$) (TABLE 5). In comparing seeds carried away from tree species, we observed no significant differences (one-way ANOVA, $F_{4,66} = 1.70$, $P > 0.05$). Other frequently used estimators of primary seed dispersal were not correlated with fruit characteristics (TABLE 5), except frequency of animal visitation and fruit size ($r = -0.853$, $P < 0.05$), frequency of animal visitation and seed size ($r = -0.828$, $P < 0.05$), and fruit mass and percentage of fruits taken relative to the fruit crop size ($r = -0.906$, $P < 0.05$).

Frugivory

A total of 33 species of birds and 2 species of primates were recorded feeding on fruits of the trees at the study site (APPENDIX 1). Frugivore species that dispersed the highest percentage of *Hebepetalum humiriifolium* seeds were the white-throated toucan (*Ramphastos tucanus* Ramphastidae), some araçaris (*Pteroglossus* spp. Ramphastidae), and the black-necked red cotinga (*Phoenicircus nigricollis* Cotingidae). The blue-crowned motmot (*Momotus momota* Momotidae) dispersed a high percentage of seeds of *Roucheria columbiana* and *Ocotea* sp. Primates (*Saguinus fuscicollis* Callithrichidae), trogons (*Trogon melanurus* and *T. viridis* Trogonidae), and the white-throated toucan were the leading dispersers of *Micropholis venulosa* seeds. The collared titi (*Callicebus torquatus* Cebidae), the bare-necked fruit crow (*Gymnoderus foetidus* Cotingidae), and the black-tailed tityra (*Tityra cayana* Cotingidae) were major dispersers for *Trattinnickia* sp.

Some frugivore species were observed more

TABLE 6. Extended.

Ocotea sp.			*Micropholis venulosa*			*Trattinnickia* sp.		
N	No. individuals per visit	Frugivore contribution (% seeds carried away)	*N*	No. individuals per visit	Frugivore contribution (% seeds carried away)	*N*	No. individuals per visit	Frugivore contribution (% seeds carried away)
3	1.00	3.92	7	1.20	2.64	3	1.01	0.53
4	1.00	4.90	13	1.00	1.39	0		
12	1.00	23.04	2	1.00	7.77	11	1.40	3.39
3	1.67	5.73	1	1.00	0.40	8	1.17	1.29
4	2.00	8.82	2	1.00	0.20	4	1.06	0.84
2	2.70	4.21	0			9	1.87	2.07
4	2.51	4.48	0			6	1.40	0.44

than two times, feeding on fruits of at least four of the five tree species (TABLE 6). These common frugivores were two species of trogons (*Trogon melanurus* and *T. violaceus*), the white-throated toucan, two cotingas, and two thrushes (*Turdus ignobilis debilis* and *T. obsoletus*). The white-throated toucan, the black-tailed and the violaceous trogons, and the purple-throated fruit crow were the leading contributors to seed dispersal, visiting all tree species more than twice. In contrast, primary seed dispersal contributed by *Phoenicircus nigricollis, Turdus ignobilis debilis,* and *T. obsoletus* in some trees was not significant (with none or less than two recordings per species).

Feeding behaviors, such as number of visits and fruit-handling times, performed by these common frugivores were significantly different among tree species ($F_{4,32} = 2.91$, $P < 0.05$; $F_{4,32} = 3.76$, $P < 0.05$, respectively). Number of visits at *Hebepetalum humiriifolum* were significantly higher than were number of visits at trees with larger fruit sizes and firm pulp, such as *Micropholis venulosa* ($q_{32,5} = 4.13$, $P < 0.05$) and *Ocotea* sp. ($q_{32,5} = 4.13$, $P < 0.05$). Fruit-handling times at *Trattinnickia* sp, *M. venulosa,* and *Ocotea* sp. were longer than were fruit-handling times of *H. humiriifolium,* the tree species with the smallest fruit sizes ($q_{36,5} = 4.29$, $P < 0.05$, $q_{36,5} = 5.09$, $P < 0.05$, $q_{36,5} = 5.11$, $P < 0.05$, respectively). Feeding behaviors such as the proportion of fruits taken, the proportion of seeds dropped and carried away, feeding rates, and visit length did not show significant differences among trees ($F_{4,32} = 1.44$, $P > 0.05$; $F_{4,32} = 0.96$, $P > 0.05$; $F_{4,32} = 1.87$, $P > 0.05$; $F_{4,31} = 2.26$, $P > 0.05$; $F_{4,31} = 0.85$, $P > 0.05$; respectively).

When analyzing feeding behaviors of the common frugivores, we found that some of these behaviors were significantly affected by any fruit characteristic (APPENDIXES 2 & 3). Fruit-handling times of *Trogon melanurus* increased with fruit size ($r = 0.895$, $P < 0.05$). Feeding rates and fruit-handling times of *Ramphastos tucanus* were significantly affected by seed size ($r = -0.956$, $P < 0.05$, $r = 0.875$, $P < 0.05$, respectively). In addition, seeds dropped by *Querula purpurata* were significantly correlated by fruit size ($r = -0.919$, $P < 0.05$) and pulp content ($r = 0.841$, $P < 0.05$). Correlations relative to the bigger the seed size, the lower the *Q. purpurata* feeding rates ($r = 0.966$, $P < 0.05$) also existed.

DISCUSSION

In our study, diurnal frugivores were responsible for 12–32% of total fruit crop reduction among the studied trees. During diurnal frugivory, the percentage of seeds leaving the tree relative to the fruits taken by frugivores, with feeding behavior included in the calculations, was a good estimator of primary seed dispersal. However, previous studies (McKey 1975, Howe 1982, 1990, Janson 1983, Wheelwright 1985, 1993, Levey 1986, Murray 1987) found that estimators, such as the number and frequency of frugivores and proportion of fruits taken, were not good predictors of seed dispersal. Thus, such indicators might reflect some differences among plant species, such as fruit crop sizes, fruit types, and fruit availability of a forest. For instance, the highest number of animal species at the tree crown and the highest proportion of fruits taken were recorded in *Trattinnickia* sp. and *Hebepetalum humiriifolium,* tree species that exhibited the largest fruit crop sizes and soft-juicy fruits. Moreover, *Trattinnickia* sp. fruited when a period of low availability within the forest occurred, while *Ocotea* sp., *H. humiriifolium, Roucheria columbiana,* and *Micropholis venu-*

losa fruited during the fruiting peak of the forest (A. Parrado-Rosselli unpubl. data). The percentage of *Trattinnickia* sp. seeds carried away from the parent tree (primary seed dispersal), however, was the lowest of that observed among the studied trees. Thus our results agree with Jordano and Schupp (2000), who stated that whether fruit consumption leads to successful seed dispersal (away from the parent canopy) depends largely on fruit crop size, frugivore feeding behavior, fruit processing, and post-feeding movements of animals.

Primary seed dispersal was affected more by fruit size than by any other fruit characteristic, as suggested in earlier studies on frugivory in other tropical rain forests (Howe & Smallwood 1982, Howe 1982, Herrera 1986, Wheelwright 1985, 1993). Although seed size, fruit mass, and percentage of pulp analyzed separately did not affect primary seed dispersal, other studies found these characteristics to have an important effect on seed dispersal (Howe & Smallwood 1982, Wheelwright 1985, Herrera 1986, Levey 1986, 1987, Moermond et al. 1986, Fleming et al. 1993, Martinez del Rio & Restrepo 1993). In addition, although differences seem to exist between the largest and the smallest fruit-sized tree species, we found no significant differences when analyzing whether mean primary seed dispersal was different among trees. Real consequences of fruit size for seed dispersal might be more evident in comparisons of a broader range of fruit-sized plant species.

Frugivores and their Role as Seed Dispersers

Fruit-eating animals varied among focal tree species in their roles as seed dispersers. The white-throated toucan, two cotingas, two trogons, and two thrushes are suggested as good primary seed dispersers of at least four of the five tree species studied. These animals visited the trees on a regular basis and showed a higher percentage of seeds carried away than did other frugivores feeding on the same trees. Good dispersers stayed less than 6 min. in any fruiting tree, increasing the number of seeds potentially dispersed by diminishing the probability of regurgitating or defecating seeds beneath the parent plant (Howe 1982, Schupp 1993). Findings on toucans are consistent with previous studies that suggested these birds as leading seed dispersers in tropical rain forests (Snow 1981, Kubitzki 1985, Guevara & Laborde 1993, Howe 1993, Galleti et al. 2000). Some studies suggested that the seed dispersal capacity of some cotingas and thrushes resulted from their facility in handling fruits and the mild processing of fruits and seeds during digestion (Snow 1976, 1981, Kubitzki 1985, Guevara & Laborde 1993). Other birds, however, were good dispersers for a single tree species, where handling may have been facilitated by fruit size. Opportunistic frugivores considered to be poor dispersers may contribute to primary seed dispersal, because their behavior of selecting only a few fruits diminishes the possibility of finding more than two seeds in a fecal aggregate. Parrots and macaws (Psittacidae), usually considered seed predators, also may carry seeds away from the tree crown either by ingestion or by accidental transport (A. Parrado-Rosselli pers. obs.). In addition, some animals may be secondarily removing seeds from the tree crown. For example, species such as gray-winged trumpeter birds (*Psophia crepitans* Psophidae), curassows (*Crax* spp Cracidae), and such mammals as agoutis (*Dasyprocta* spp., Dasyproctidae & *Agouti* spp., Agoutidae) were observed foraging under the crown of the focal trees (A. Parrado-Rosselli pers. obs).

Effect of Fruit Size on Feeding Behavior

Some feeding behaviors of frugivores were heavily influenced by fruit size. This relationship was evident for the animals that visited all focal tree species, since their fruit- handling times were longer when fruit size was bigger, and more feeding visits were recorded at the smallest fruit sized species *Hebepetalum humiriifolium* than at the larger fruit sized *Ocotea* sp. and *Micropholis venulosa*. On the other hand, although the percentage of fruits taken, seeds dropped and carried away, feeding rates, and visit length were not significantly different among focal trees, our correlation analysis of each frugivore feeding behavior revealed varied effects of the different fruit characteristics considered in this study. According to Jordano and Schupp (2000), frugivore feeding and fruit-handling behaviors are largely species-specific characteristics. A single fruit trait, thus, does not necessarily predict a frugivore feeding behavior or its contribution to seed dispersal. Factors such as digestive rates, time of seed and fruit passage, and breeding periods are valuable in determining the amount of fruit consumed and a frugivore behavior (Levey 1986, Fleming et al. 1993, Martinez del Rio & Restrepo 1993, Pratt & Stiles 1983). Fruit size, which appears to have a significant effect on fruit-handling times, can be most valuable in determining the number of fruits that can be removed, handled, and ingested by an animal during a feeding bout. Consequently, fruit characteristics, particularly fruit size, can provide insights on the possible behavior of frugivores and their role as seed dispersers.

Finally, although potential post-dispersal events may cause different seed and seedling distributions (Nathan & Muller-Landau 2000), some studies have concluded that frugivore activity and behavior affect not only seed dispersal but may shape the spatial pattern of seedling establishment and spatial distribution of trees (Janzen 1970, Connell 1971, Bleher & Böhning-Gaese 2001). To better understand the relative impact of primary and secondary seed dispersal by animals on seedling and adult tree distribution, future studies need to assess seed dispersal by considering not only fruit removal but also frugivore feeding behavior.

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APPENDIX 1. General results on frugivory and primary seed dispersal of five tree species studied in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996. Percentage of fruits taken, seeds taken away, and non-dispersed (dropped and damaged) for each animal species visiting the focal plant. Scientific names and order of species are sensu Hilty and Brown (1986) and Emmons and Feer (1990).

Frugivores		*Trattinnickia* sp.		
Family	Species and common names	Fruits taken %	Seeds taken away %	Seeds non-dispersed %
Legitimate frugivores				
Trogonidae	*Trogon melanurus* (Black-tailed trogon)	0.53	0.53	0.00
	Trogon violaceus (Violaceous trogon)			
	Trogon viridis (White-tailed trogon)	1.42	1.11	0.32
	Trogon sp.			
Momotidae	*Momotus momota* (Blue-crowned motmot)			
Capitonidae	*Capito niger transilens* (Black-spotted barbet)	0.37	0.32	0.05
	Eubucco richardosoni (Lemon-throated barbet)	0.84	0.53	0.32
Ramphastidae	*Ramphastos tucanus* (White-throated toucan)	4.84	2.42	2.42
	Pteroglossus flavirostris (Ivory-billed aracari)	0.53	0.53	0.00
	Pteroglossus inscriptus (Lettered aracari)			
	Pteroglossus pharicinctus (Many-banded aracari)			
Pipridae	*Pipra erythrocephala* (Golden-headed manakin)			
	Pipra sp.	0.16	0.16	0.00
	Tyranneutes stolzmanni (Dwarf-tyrant manakin)			
Cotingidae	*Phoenicircus nigricollis* (Black-necked red cotinga)	1.32	1.11	0.21
	Pachyramphus polychopterus (White-winged becard)	0.89	0.68	0.21
	Tityra cayana (Black-tailed tityra)	5.89	5.00	0.89
	Porphyrolaema porphyrolaema (Purple-throated cotinga)	0.58	0.58	0.00
	Cotinga cayana (Spangled contінga)	0.79	0.00	0.79
	Gymnoderus foetidus (Bare-necked fruitcrow)	4.89	4.10	0.79
	Querula purpurata (Purple-throated fruitcrow)	0.84	0.79	0.05
Tyrannidae	*Pitangus sulphuratus* (Great kiskadee)	0.47	0.47	0.00
Corvidae	*Cyanocorax violaceus* (Violaceous jay)	0.79	0.16	0.63
Turdidae	*Trudus ignobilis debilis* (Black-billed thrush)	1.74	1.11	0.63
	Turdus obsoletus (Pale-vented thrush)	1.00	0.32	0.68
	Turdus albicollis (White-necked thrush)			
	Turdus sp.			
Thraupidae	*Euphonia laniirostris* (Thick-billed euphonia)			
Predators				
Cracidae	*Aburria pipile* (Common piping-guan)			
Columbidae	*Columba plumbea* (Plumbeous pigeon)			
	Columba sp.	0.84	0.00	0.84
Psittacidae	*Ara macao* (Scarlet macaw)	69.70	0.00	69.70
	Pionus menstruus (Blue-headed parrot)			
Primates				
Callithrichidae	*Saguinus fuscicollis* (Saddle-back tamarin)			
Cebidae	*Callicebus torquatus* (Collared titi)	1.58	0.84	0.74

APPENDIX 1. Extended.

Ocotea sp.			*Roucheria columbiana*			*Hebepetalum humiriifolium*			*Micropholis venulosa*		
Fruits taken %	Seeds taken away %	Seeds non-dispersed %	Fruits taken %	Seeds taken away %	Seeds non-dispersed %	Fruits taken %	Seeds taken away %	Seeds non-dispersed %	Fruits taken %	Seeds taken away %	Seeds non-dispersed %
3.92	3.92	0.00	3.07	2.76	0.00	1.85	1.70	0.15	2.90	2.20	0.70
5.88	4.90	0.98	2.76	2.45	0.31	0.81	0.81	0.00	4.64	1.39	3.25
			0.31	0.31	0.00	0.30	0.30	0.00	1.16	0.81	0.35
			0.92	0.92	0.00						
0.98	0.98	0.00	11.35	10.74	0.61						
						0.82	0.82	0.00			
						0.32	0.32	0.00			
			22.70	19.63	3.07	19.57	14.70	4.58	16.47	7.77	7.89
33.82	23.04	10.78									
1.98	1.58	0.40				8.96	8.28	0.68	1.02	0.53	0.49
2.92	1.48	1.44				13.79	12.82	0.97			
			0.31	0.00	0.31	0.32	0.32	0.00			
						0.44	0.15	0.30			
						0.52	0.52	0.00			
3.92	3.43	0.49	11.35	8.59	2.45	11.97	11.67	0.22	0.70	0.40	0.30
9.26	5.78	3.47									
7.84	2.94	4.90	1.23	1.23	0.00	1.63	1.33	0.00	4.23	0.00	4.23
4.41	4.41	0.00	2.15	2.15	0.00	3.55	2.59	0.96	0.20	0.20	0.00
			0.31	0.31	0.00	1.47	1.40	0.07			
6.82	1.92	4.90							9.30	0.00	9.30
2.45	1.56	0.89	24.23	15.64	8.28	7.61	5.32	1.55			
2.93	1.94	0.99	17.79	7.36	10.43	2.95	2.59	0.22			
			0.61	0.00	0.61	1.92	1.48	0.44			
			0.92	0.61	0.31						
						0.72	0.42	0.30			
						20.51	0.00	20.51			
7.90	0.00	7.90									
4.95	0.00	4.95							12.74	0.00	12.74
									14.44		14.44
									32.20	20.67	11.53

APPENDIX 2. Pearson product-moment correlation coefficients (r) between fruit characteristics and feeding behavior of frugivores that visited more than twice the five tree species studied in a terra firme forest site along the Caquetá River, Amazonas Colombia, 1996. Boldface figures, $P < 0.05$.

Frugivores			Feeding behaviors					
Family	Species (common name)	Fruit characteristics	Fruits taken (%)	Seeds carried away (%)	Seeds dropped (%)	Feeding rate (No. fruits/min)	Fruit handling time (s)	Visit length (s)
Trogonidae	*Trogon melanurus* (Black-tailed trogon)	Fruit size (cm)	0.028	−0.022	0.233	0.120	**0.895**	0.117
		Seed size (cm)	0.217	0.201	0.429	−0.680	0.760	0.338
		Fruit weight (g)	0.644	0.489	0.642	−0.192	0.713	0.454
		% of Pulp	0.019	−0.065	0.100	0.599	0.563	−0.002
Ramphastidae	*Ramphastos tucanus* (White-throated toucan)	Fruit size (cm)	−0.256	−0.392	0.169	−0.526	0.607	0.408
		Seed size (cm)	0.101	−0.201	0.747	**−0.956**	**0.875**	0.527
		Fruit weight (g)	0.273	0.117	0.476	−0.305	0.750	0.766
		% of Pulp	−0.297	−0.253	−0.275	0.083	0.181	0.245
Cotingidae	*Querula purpurata* (Purple-throated fruitcrow)	Fruit size (cm)	−0.607	−0.415	**−0.919**	−0.501	−0.075	0.296
		Seed size (cm)	−0.121	−0.022	−0.418	**−0.966**	0.740	0.396
		Fruit weight (g)	−0.395	−0.250	−0.674	−0.270	0.060	−0.262
		% of Pulp	−0.678	−0.511	**−0.841**	0.126	−0.632	−0.065

APPENDIX 3. Pearson product-moment correlation coefficients (r) between fruit characteristics and feeding behavior of frugivores that visited, more than twice, four of the five tree species studied in a terra firme forest site along the Caquetá River, Amazonas, Colombia, 1996. Boldface figures, $P < 0.05$. ND = not determined.

Frugivores			Feeding behaviors					
Family	Species (common name)	Fruit characteristics	Fruits taken (%)	Seeds carried away (%)	Seeds dropped (%)	Feeding rate (No. fruits/min)	Fruit handling time (s)	Visit length (s)
Trogonidae	*Trogon violaceus* (Violaceous trogon)	Fruit size (cm)	**0.860**	0.431	**0.799**	−0.253	**0.931**	0.557
		Seed size (cm)	**0.823**	0.419	0.727	**−0.885**	0.755	0.714
		Fruit weight (g)	0.689	0.166	0.836	−0.192	0.793	0.647
		% of Pulp	0.377	0.128	0.412	0.397	0.529	0.164
Contingidae	*Phoenicircus nigricollis* (Black-necked red-cotinga)	Fruit size (cm)	**−0.850**	**−0.931**	−0.022	**−0.905**	−0.205	ND
		Seed size (cm)	**−0.872**	**−0.815**	−0.661	**−0.830**	0.591	ND
		Fruit weight (g)	−0.388	−0.488	0.280	−0.688	0.204	ND
		% of Pulp	−0.352	−0.509	0.551	−0.520	−0.619	ND
Turdidae	*Turdus ignobilis debilis* (Black-billed thrush)	Fruit size (cm)	−0.185	−0.215	−0.041	**−0.941**	**0.896**	−0.149
		Seed size (cm)	**−0.836**	**−0.849**	−0.764	−0.704	0.056	0.053
		Fruit weight (g)	0.530	0.509	0.624	−0.523	0.483	**−0.948**
		% of Pulp	0.481	0.456	0.593	−0.556	**0.957**	−0.342
	Turdus obsoletus (Pale-vented thrush)	Fruit size (cm)	−0.015	−0.206	0.117	−0.721	0.753	0.714
		Seed size (cm)	−0.713	−0.748	−0.667	−0.411	−0.173	−0.228
		Fruit weight (g)	0.684	0.630	0.709	**−0.903**	**−0.863**	0.276
		% of Pulp	0.594	0.414	0.701	−0.596	0.506	**0.935**