



Effects of Seed Dispersal by Three Ateline Monkey Species on Seed Germination at Tinigua National Park, Colombia

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*We examined the effect of seed ingestion by three ateline primates: woolly monkeys, *Lagothrix lagothricha*; spider monkeys, *Ateles belzebuth*; and, red howler, *Alouatta seniculus* on germination rates and latency periods of seeds of several plant species in Tinigua National Park, Colombia. We collected dispersed seeds from feces and control seeds from the parental trees and washed them for germination trials. For the majority of plants, dispersed seeds germinated as well or better than control seeds did. Although spider monkeys depend more heavily on fruits than the other monkey species do, they were not more efficient than howlers or woolly monkeys at improving germination rates. A considerable proportion of the seeds dispersed by howlers and woolly monkeys showed reduced latency periods to germination, but spider monkeys showed less effect on reducing germination time. This result may be related to longer gut retention times, but such a trend has not been observed in other primate species. We conclude that, like many other primates, ateline monkeys are effective seed dispersers in terms of their effects on the seeds they swallow*

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because they rarely decrease their germination rates. We discuss problems that make interspecific comparisons difficult, such as inappropriate control seeds and differences associated with germination substrates, and we stress the importance of studying other components of seed dispersal effectiveness.

KEY WORDS: germination rate; *Lagothrix lagothricha*, *Ateles belzebuth*, *Alouatta seniculus*; latency period; seed dispersal.

INTRODUCTION

The effectiveness of primates as seed dispersers has been unclear since the first studies on the topic in the 1980s. For example, pioneering studies indicated that spider monkeys deposit seeds in clumps beneath parental trees (Howe, 1980), where the seeds may attract more predators and suffer higher intraspecific competition than seeds dispersed away from parental trees (Connell, 1971; Janzen, 1970). In contrast, other studies, including the *Ateles* species considered to be seed wasters by Howe (1980), showed that primates may be effective seed dispersers for a variety of plant species because they disperse large quantities of seeds, some of which are further dispersed by dung beetles (Chapman, 1989; Estrada and Coates-Estrada, 1984, 1991). In fact, several researchers showed that secondary dispersal by beetles reduces the probability of seed predation by rodents (Andresen, 1999; Estrada and Coates-Estrada, 1991 Shepherd and Chapman, 1998). Primates also disperse large seeds (Garber, 1986), which have a restricted assemblage of potential dispersers.

Different species of primates may play dissimilar roles as seed dispersers (Chapman, 1995; Lambert and Garber, 1998; Norconk *et al.*, 1998). For instance, in a single locality, cercopithecoid monkeys may act primarily as seed spitters, while chimpanzees are mainly seed swallows (Lambert, 1999), and the two handling treatments affect the places and densities in which seeds are dropped. Furthermore, there can be variation in the role that a single species may play depending on seasonal periods and plant species (Kaplin and Moermond, 1998).

As the number of studies on seed dispersal by primates increases, a major challenge is to find patterns that enable us to predict the potential effects that the loss of a primate species may have on plant regeneration in particular ecosystems. The main difficulty is to assess how effectively different seeds are dispersed by primate species, because seed dispersal effectiveness depends on a variety of processes such as dispersal quality and quantity (Schupp, 1993). The quantity of seed dispersal refers to the total number of seeds removed, which is the product of the number of visits made by the dispersers and the number of seeds removed per visit. The quality of seed

dispersal depends on two principal components: (1) the treatment that the seeds receive from the disperser—hands, beak or mouth, and gut—which may affect germination capability after gut passage; and (2) the density of seeds in the deposition and other characteristics of the deposition site which must be adequate for seedling development, e.g., low predation conditions or appropriate light availability.

Ateline monkeys are very effective dispersers in terms of the quantity of seeds dispersed (Chapman, 1989, 1995; Julliot, 1996; Stevenson, 2000). However, within the clade, the more folivorous howlers tend to disperse fewer seeds from a smaller set of plant species than the more specialized frugivores, such as the spider monkeys (Andresen, 1999). We compared some general patterns of seed dispersal by 3 sympatric ateline species—*Lagothrix lagothricha*, *Ateles belzebuth* and *Alouatta seniculus*—emphasizing their effects on two components of seed dispersal quality: germination rates and latency period of seeds. Germination rate is the probability that a seed will germinate, usually expressed as a percentage. Latency period is the time between experimental setup and radicle emergence from the seed.

There are alternative views about the evolutionary processes between plants and frugivores. One originated from ideas of Howe and Estabook (1977) and Snow (1971), who postulated that different dispersal systems might have evolved in response to effective seed dispersal by specialized frugivores. The theory is that some plant species produce few, high quality fruits (rich in lipids) over extended periods, which helps to maintain populations of specialized frugivores that prefer fruits instead of other dietary items. In turn, the animals act as effective dispersers for the plant species by providing good dispersal quality to the seeds (McKey, 1975). Although the hypothesis is difficult to test because little is known about the fate of seeds dispersed by different vectors (Howe, 1993), the framework offers some specific predictions that can be tested within the atelines. Spider monkeys (*Ateles* spp.) are the most specialized frugivores within the subfamily (Peres, 1994), because their basic diet consists mainly on ripe fruits and is complemented with a low proportion of leaves, flowers and some seeds. They rarely ingest animal matter. Howlers (*Alouatta* spp.) rely more on foliage than the other members of the clade do and may eat only leaves during some periods of the year (Stevenson *et al.*, 2000a). Woolly monkeys (*Lagothrix* spp.) seem to represent intermediate dietary specialization, because many fruit species comprise the main part of their diet, but they supplement it with young leaves and unripe fruits, and in some populations they spend significant time searching for animal prey (Stevenson *et al.*, 1994). Although these patterns vary between and among populations (Chapman, 1987), the dietary differences among species have been documented extensively, and even when they are studied sympatrically they show the above-mentioned

dietary preferences (Andresen, 1999; Guillotin *et al.*, 1994; Stevenson *et al.*, 2000a). Therefore, if specialized systems evolved the Atelinae, we expect to find a gradient of effective seed treatment associated with germination rates, highest in *Ateles*, intermediate in *Lagothrix*, and lowest in *Alouatta*.

The alternative hypothesis is based on prevailing ideas about the evolution of the seed-disperser mutualism, that consider it unlikely that there is a close relationship between plants and dispersers (Chapman, 1995; Herrera, 1986; Jordano, 1995). Accordingly, it would not be surprising to find disparate effects among different primates on seed germination.

Although seed dispersal effectiveness is a complex concept involving several stages in the life history of plants (Schupp, 1993), we focused only on traits related to germination success. We consider high germination rates and low latency periods as components of effective dispersal because a decrease in germination rates implies a lower chance of increasing parental plant fitness, independently of other components of seed dispersal effectiveness. Low latency periods can also be important because in tropical forests post dispersal predation can be severe for many plant species (i.e. De Steven & Putz, 1984; Howe *et al.*, 1985; Schupp, 1988). For instance, for 3 out of 4 plant species dispersed by monkeys at Tinigua, seed removal rates from the original defecation sites vary between 82 and 100 % in the first 2 mo after experimental setup (P. Stevenson, unpublished results). These results suggest the importance of rapid germination for improved plant fitness, given that effective secondary dispersal by dung beetles is restricted to small seeds (Andresen, 1999; Estrada and Coates-Estrada, 1991; Stevenson *et al.*, unpublished) and removed seeds are primarily consumed by rodents or carried to inappropriate sites for development, i.e. > 20 cm below soil surface.

It is possible that germinated seeds of some species are also predated, so at this point we lack data to strictly test our assumption that rapid seed germination increases plant fitness in this community. Yet, from our observations of high levels of seed predation in the field, we believe that it is safe to assume that rapid germination can be advantageous. Also, theoretical models predict the presence of a seedling bank instead of a seed bank in constant environments (Rees, 1994). At least for some species at Tinigua, seedling survival is higher than seed survival on the forest floor (Stevenson, pers.obs.), and plant regeneration in tropical lowland forests is mainly the product of a seedling bank rather than a seed bank (Uhl *et al.*, 1988).

The specific goals of our study were to answer the following questions: (1) How many plant species does each Tinigua ateline species disperse? (2) Do the more specialized frugivores increase germination rates more than the less specialized primates do? (3) Do differences in the latency period of seeds depend on the dispersal vector? (4) How important is the germination protocol in affecting results of germination experiments? and (5) What are

the trends in germination capabilities of seeds dispersed by other primate species as reported in the literature?

METHODS

Study Site

We conducted the study in a tropical rain forest on the eastern border of Tinigua National Park, west of Sierra de La Macarena, Departamento del Meta, Colombia. The study site is located on the western margin of the Río Duda (2°40' North and 74°10' West, 350–400 m above sea level), at the CIEM (Centro de Investigaciones Ecológicas La Macarena), in the upper Amazon basin. There is a dry season from December to February and a distinctive peak in the community-wide fruiting pattern usually between March and May (Stevenson *et al.*, 1994).

Data Collection

Seed and Feeding Samples

We collected seeds from fecal samples in different years for each primate species (1996–1997 for *Lagothrix lagothricha*, 1992 for *Ateles belzebuth*, and 1991 for *Alouatta seniculus*), while we studied other aspects of their ecology. We observed feeding behavior and performed germination experiments in 5–12-mo study periods for each ateline species. In all cases we included the season of highest fruit production. Total contact time with the primates varied between 720 h for *Lagothrix lagothricha* and 900 h for *Alouatta seniculus*.

We collected defecated seeds from feces on the ground and surrounding vegetation while following focal monkeys. We stored the seeds in plastic bags, water-washed them for germination trials, and identified them. We identified most plant species based on the fruit guide of the study site (Stevenson *et al.*, 2000b), and deposited voucher specimens in several botanical gardens in Colombia and USA (COL, COAH, MO, and NYBG).

Additionally, P Stevenson and collaborators collected dietary data for all ateline species simultaneously for an annual cycle in 1990–1991 (Stevenson *et al.*, 2000a). We recorded fruit characteristics for all plant species consumed by the monkeys, including fruit type, external color, and a count or estimation of the number of seeds per fruit. We also used phenological transects to estimate fruit production in the forest (Stevenson *et al.*, 1998).

We collected nondispersed control seeds from fruits in good condition under the crowns of parental trees. We removed the pulp around the

seeds by hand and water-washed the seeds for germination trials. We define germination of a seed as the moment the radicle appears.

Germination Setup and Substrates

We performed germination trials in different years and used different germination substrates for the seeds defecated by the primate species. We used forest soil in plastic containers with appropriate drainage for the seeds dispersed by *Ateles belzebuth*. We covered the plastic containers with fine mesh to protect them from predation. For the seeds defecated by *Lagothrix lagothricha*, we used moist cotton tissue in petri dishes. We planted some of the species dispersed by *Alouatta seniculus* in soil and some on cotton tissue. In the latter case, we protected the plastic containers from predators with a nylon mesh. In all cases, we kept the samples under humid conditions and protected from direct sunlight.

We set to germinate ≤ 10 seeds of the same species in the same container—plastic or petri dish—separating the treatments: defecated or control. We obtained data from several containers for each seed species. We tried to keep all containers under the same conditions.

Statistical Analyses

We constructed a 2×2 contingency table for each plant species to test for independence between type of seed—dispersed versus non-ingested controls—and germination success: yes vs. no. We analyzed the tables via Fisher's exact tests when the total number of seeds for each treatment was fixed and the sample size was small ($n < 50$). Otherwise, we used G-tests of independence (Sokal and Rohlf, 1995). We also compared the mean effect on rates of germination among primate species via a Kruskal-Wallis ANOVA. We used the same analyses for some plant species dispersed by different primates, in order to test for differences in germination success in different germination substrates. We used Mann-Whitney U-tests to assess differences in latency period between defecated and control seeds.

RESULTS

Number of Dispersed Species

Lagothrix and *Ateles* consume and remove seeds of more plant species than *Alouatta* does (Appendix). For example, 84% and 83% out of the

90 most consumed fruit species (in terms of time spent in fruiting trees, Appendix) in this community are at least sometimes dispersed by *Logothrix lagothricha* and *Ateles belzebuth*, respectively, while *Alouatta seniculus* is a potential disperser of 53% of them. The 3 ateline species are also potential predators – a low proportion of the species (*Logothrix*, 16%, *Ateles*, 10% and *Alouatta*, 6%) are predated sometimes, only under particular conditions. For a few plant species they always act as seed predators (*Logothrix*, 6%, *Ateles*, 2%, and *Alouatta*, 1%). The same trend occurred during the period of highest fruit production, when our germination experiments took place; *Ateles* consumed fruits belonging to 71 species, *Logothrix* ingested 78 species, and *Alouatta*, 22 species.

Germination Rates

Table I shows the results for plant species for which it was possible to get a sample size of ≥ 15 to compare germination rates between defecated and noningested seeds. In general, the seeds dispersed by *Ateles* showed few changes in germination rates between defecated and control seeds, as indicated by the average germination rate across plant species (Table I). Out of 14 species, 6 had significantly higher germination rates for defecated seeds, 4 indistinguishable rates, and 4 lower rates than control seeds. In contrast, the majority of species analyzed for *Logothrix* showed higher than (8 spp.) or similar germination rates (7 spp.) to those of control seeds, while only one species had lower germination. A similar trend characterizes the seeds dispersed by *Alouatta*, where most of the species had higher germination rates (4), a few had indistinguishable rates (2), and in only one case control seeds had higher germination rates than defecated seeds. For one of the species dispersed by howlers—*Guapira cf. cuspidata*—endozoochory was necessary to induce germination, given that none of the control seeds germinated.

A Kruskal-Wallis ANOVA showed no significant difference in the mean effect of dispersal on germination (% defecated - % control seeds; last column of Table I) among the 3 ateline species ($H = 1.49$, $p = 0.47$).

We have enough data for only one species (*Castilla ulei*) dispersed by all three monkeys. Dispersed seeds by all of the primates had lower germination rates than those of control seeds, though the difference is not significant for the seeds dispersed by woolly monkeys. In 3 other plant species dispersed by woolly and spider monkeys (*Simarouba amara*, *Inga edulis*, and *Protium sagotianum*), there was higher germination in seeds defecated by them versus controls (Table I). However, for the latter two seed species the difference is not significant in one of the primate species. Finally, there is one case (*Ficus*

Table I. Germination rates as the percentages of dispersed and control seeds that germinated in trials

Primate species	Plant species	Germination Rate (%)				Difference ^a	
		Dispersed	N	Control	N		
<i>Ateles</i> <i>belzebuth</i>	<i>Alibertia cf. handrantha</i>	95	44	95	40	0	n.s.
	<i>Brosimum lactescens</i>	47	32	89	28	-42	*
	<i>Brosimum alicastrum</i>	76	29	45	31	31	*
	<i>Castilla ulei</i>	39	82	100	24	-61	*
	<i>Coussapoa orthoneura</i>	22	363	60	100	-38	*
	<i>Ficus pertusa</i>	45	308	8	280	37	*
	<i>Inga edulis</i>	87	15	78	23	9	n.s.
	<i>Jacaratia digitata</i>	0	29	0	20	0	n.s.
	<i>Leonia crassa</i>	100	39	100	25	0	n.s.
	<i>Oenocarpus bataua</i>	94	17	50	20	44	*
	<i>Protium crenatum</i>	25	12	13	15	12	n.s.
	<i>Protium sagotianum</i>	33	51	15	52	18	*
	<i>Simarouba amara</i>	89	18	10	21	79	*
	<i>Trichilia tuberculata</i>	80	35	55	42	25	*
	<i>Trichostigma octandrum</i>	35	17	97	32	-62	*
	Average					3.5	
<i>Lagothrix</i> <i>lagothricha</i>	<i>Apeiba aspera</i>	32	90	28	90	4	n.s.
	<i>Castilla ulei</i>	30	60	42	60	-12	n.s.
	<i>Cecropia sciadophylla</i>	54	90	43	90	11	n.s.
	<i>Crepidospermum rhoifolium</i>	52	60	10	60	42	*
	<i>Ficus insipida</i>	67	90	70	90	-3	n.s.
	<i>Ficus nymphaeifolia</i>	46	90	4	90	42	*
	<i>Gustavia hexapetala</i>	43	70	45	60	-2	n.s.
	<i>Helicostylis tomentosa</i>	55	60	5	60	50	*
	<i>Hyeronima alchorneoides</i>	23	60	10	60	13	n.s.
	<i>Inga alba</i>	58	60	7	60	51	*
	<i>Inga edulis</i>	67	60	7	60	60	*
	<i>Pourouma bicolor</i>	80	70	50	60	30	*
	<i>Protium sagotianum</i>	42	60	32	60	10	n.s.
	<i>Pseudolmedia laevigata</i>	25	60	4	50	21	*
	<i>Sarcaulus brasiliensis</i>	46	50	77	30	-31	*
<i>Simarouba amara</i>	55	50	13	40	42	*	
	Average					20.5	
<i>Alouatta</i> <i>seniculus</i>	<i>Castilla ulei</i>	67	60	92	92	-25	*
	<i>Coccoloba densifrons</i>	33	129	35	129	-2	n.s.
	<i>Ficus insipida</i>	63	200	20	200	43	*
	<i>Inga acreana</i>	100	40	75	40	25	*
	<i>Inga cylindrica</i>	100	130	100	130	0	n.s.
	<i>Guapira cf. cuspidata</i>	37	175	0	175	37	*
	<i>Pseudolmedia laevis</i>	61	90	17	90	44	*
	Average					17.4	

^aBetween dispersed and control seeds.

Note. The different plant species were ingested by 3 ateline species in Tinigua National Park, Colombia. N = seed sample size. The last column shows the difference in germination rate between dispersed and control seeds—a positive number implies higher germination after dispersal by the monkeys. Statistically significant differences at $\alpha = 0.05$ are followed by an asterisk (n.s. = non-significant differences).

insipida) in which the effect of dispersal by howler and woolly monkeys seemed to have opposite effects on germination rates.

Latency Periods

The majority of the species dispersed by *Ateles* (9 of 14) had similar latency periods as control seeds (Table II), while a few plant species were significantly different in time to germination: one with a reduced period and two with a longer period. In the case of *Lagothrix*, the distribution of the number of plant species showing longer, indistinguishable or shorter latency

Table II. Average latency period in days (± standard deviation) for control seeds and seeds of different plant species dispersed by the 3 ateline species in Tinigua National Park, Colombia

Primate Species	Plant species	Average ± SD			N	Difference ^a
		Dispersed seeds	Control seeds			
<i>Ateles belzebuth</i>	<i>Alibertia cf. hadrantha</i>	7.7 ± 2.6	9.0 ± 2.9	55	-1.3	*
	<i>Brosimum alicastrum</i>	16.2 ± 11.6	8.0 ± 0.0	36	8.2	n.s.
	<i>Brosimum lactescens</i>	22.9 ± 12.6	25.1 ± 16.6	31	-2.2	n.s.
	<i>Castilla ulei</i>	36.8 ± 22.7	33.1 ± 15.0	30	3.7	n.s.
	<i>Coussapoa orthoneura</i>	8.0 ± 4.4	11.1 ± 10.6	141	-3.1	*
	<i>Ficus pertusa</i>	14.4 ± 12.8	12.4 ± 3.9	93	2	n.s.
	<i>Inga edulis</i>	8.8 ± 7.9	8.9 ± 7.6	31	-0.1	n.s.
	<i>Leonia crassa</i>	9.1 ± 5.4	10.3 ± 7.7	47	-1.2	n.s.
	<i>Oenocarpus bataua</i>	20.6 ± 4.7	23.2 ± 4.9	26	-2.6	n.s.
	<i>Protium sagotianum</i>	15.8 ± 10.2	12.1 ± 3.0	25	3.7	n.s.
	<i>Trichilia tuberculata</i>	5.3 ± 1.4	5.9 ± 3.3	51	-0.6	n.s.
	<i>Trichostigma octandrum</i>	10.2 ± 1.2	7.1 ± 5.8	40	3.1	*
<i>Lagothrix lagothricha</i>	<i>Castilla ulei</i>	19.0 ± 7.7	24.8 ± 7.0	29	-5.8	n.s.
	<i>Cecropia membranacea</i>	10.2 ± 6.3	16.4 ± 9.1	76	-6.2	*
	<i>Crepidospermum</i>	19.7 ± 11.8	25.0 ± 0.0	37	-5.3	*
	<i>Helicostylis tomentosa</i>	38.9 ± 12.7	32.0 ± 0.0	44	6.9	n.s.
	<i>Hyeronima alchorneoides</i>	40.8 ± 6.6	34.0 ± 4.6	21	6.8	n.s.
	<i>Inga alba</i>	13.7 ± 1.8	16.8 ± 5.5	39	-3.1	n.s.
	<i>Inga edulis</i>	10.8 ± 2.1	23.0 ± 0.0	47	-12.2	*
	<i>Inga marginata</i>	8.6 ± 0.5	5.0 ± 0.0	28	3.6	*
	<i>Protium sagotianum</i>	21.7 ± 9.9	25.0 ± 0.0	40	-3.3	n.s.
<i>Alouatta seniculus</i>	<i>Castilla ulei</i>	7.5 ± 2.2	21.6 ± 8.2	95	-14.1	*
	<i>Coccoloba densifrons</i>	30.1 ± 11.6	31.4 ± 9.7	87	-1.3	n.s.
	<i>Ficus insipida</i>	8.9 ± 0.8	14.1 ± 3.5	165	-5.2	*
	<i>Inga acreana</i>	1.1 ± 0.3	2.3 ± 0.6	70	-1.2	*
	<i>Inga cylindrica</i>	3.3 ± 2.5	3.9 ± 1.8	260	-0.6	n.s.
	<i>Pseudolmedia laevis</i>	47.8 ± 15.3	57.6 ± 5.9	70	-9.8	*

^aBetween dispersed and control seeds.

Note. The last column shows the difference in average latency between dispersed and control seeds—a negative number implies faster germination after dispersal. Statistically significant differences at α = 0.05 are followed by an asterisk (n.s. = non-significant differences).

periods for dispersed seeds than for control seeds is more homogeneous (3, 4 and 2 respectively), though there is a tendency towards shorter or similar latency periods for dispersed seeds. This trend is more pronounced for the effect on latency period by howlers, given that 4 of 7 species resulted in shorter latency periods for the dispersed than those of control seeds. For two species there was similar latency, and none showed an increase in latency period with dispersal by howlers (Table II). In this case, there is no significant difference among the 3 ateline species in the mean differences in latency period between dispersed and control seeds (last column in Table II) (Kruskal-Wallis ANOVA, $H = 5.15$, $p = 0.076$). The mean difference for *Lagothrix* is closest to zero, while in *Alouatta* values are lower on average.

The trend in the effect of seed dispersal on latency period among the 3 ateline species, also appeared in the only species (*Castilla ulei*) analyzed for all 3 monkey species (Table II). Control seeds showed a non-significant tendency to germinate earlier than seeds dispersed by spider monkeys. However, the trend was opposite for woolly monkeys (although still a non-significant difference), but highly significant for the howlers.

Effect of germination substrates

For 5 species it was possible to compare the germination rates of control seeds on different substrates. In four of them (*Castilla ulei*, *Inga edulis*, *Protium sagotianum*, and *Ficus insipida*), there are significant differences in germination rates on different substrates, and for one species, (*Simarouba amara*), there is no difference (Table I).

DISCUSSION

The dispersed seeds of the majority of species germinated as well or better than control seeds, indicating the neutral or positive effects of the 3 monkey species on the plant species they consume. When we compare the mean effect of the primates on the germination of all seeds they disperse, we found no significant difference among them, but this is mainly due to high variation in the effects, *i.e.* for some species dispersal increases germination rates or latency periods, while for others it decreases them. Accordingly, considering trends on a species to species basis is more appropriate, and the results show 2 general patterns: first, the germination rates of seeds dispersed by *Ateles* are similar to those of the control seeds, while dispersal by *Alouatta* and *Lagothrix* are more often likely to increase germination rates of the defecated seeds (Table I). Second, latency time was reduced for seeds dispersed by woolly monkeys and particularly by howlers (Table II). Both results point in the same direction. In terms of germination rates, the most

specialized frugivore (*Ateles belzebuth*) has the least positive effect on seed dispersal quality, compared to more generalist primates. This is contrary to the predictions of the effective specialist disperser hypothesis (Howe and Estabook, 1977; McKey, 1975). Although spider monkeys disperse large seeds as predicted by the theory, howler and woolly monkeys also swallow large seeds (Appendix). Our only result that agrees with the hypothesis of effective specialist dispersers is that *Ateles* spent considerably more time than the other primates consuming fruits that are rich in lipids, such as *Oenocarpus* spp., *Virola* spp., and several species in the Lauraceae (Appendix). Therefore, in terms of dispersal quantity, they may be the best dispersers for these lipid-rich fruit species. In general, however, there is little evidence suggesting that they give preferential seed treatment associated with higher germination rates. Evidence against the theory has been documented for other plant-animal assemblages, in which specialized fruits, i.e., ones rich in lipids, are consumed by very ineffective dispersers (Fuentes, 1995).

Specific comparisons of the effects of the 3 ateline species on particular seed species are problematic. They share many species in their diets (Appendix), but they consume them in different proportions, so that we did not have enough comparable data for more than a few plant species.

Our data showing differences in germination rates of seeds dispersed by the different primates may be interpreted as a consequence of passage time through the gut. Seeds have relatively short retention times in spider monkey guts, hence they could have less influence on germination rates and changes in latency period compared to those of woolly monkeys and howlers, which have longer retention times (Milton, 1984). We tried to confirm the generality of this result, as reported by different studies among primates, expecting a positive correlation between retention time and both germination rates and latency periods (Table III). However, there is no significant correlation between transit time and the percentage of seed species with shorter latency periods ($r = 0.15$, $n = 6$, $p > 0.05$) or higher germination rates ($r = -0.1$, $n = 16$, $p > 0.05$). Even though it is difficult to compare the results among primate species due to the strong effect of the substrate of germination trials and the different statistical procedures used in the studies in Table III, the results suggest that the seeds consumed by different primate species respond in contrasting ways to similar physiological treatments during endozoochory. This may produce different effects on germination, even for primate species in the same genus i.e., *Alouatta* spp. (Table III), with presumably similar digestive physiology.

It is also possible that primate species affect germination rates and latency periods in different ways; however, a literature review indicated that the majority of primate species have similar effects on germination parameters. In the majority of cases, seed dispersal by primates increased

Table III. Effect of seed dispersal by several primate species on germination rates and latency periods of seeds

Primate species	Transit time	Germination rate				Time to germination				Ref ^a
		higher	ns	lower	n	higher	ns	lower	n	
<i>Eulemur rubriventer</i>	3.27	0	0	100	5					1
<i>Eulemur rubriventer</i>	3.27	50	50	0	2					2
<i>Eulemur fulvus</i>	1.57	50	50	0	2					2
Lemurs (7 species)		0	100	0	2					3
<i>Varecia</i>	1.69	0	100	0	2					2
<i>Erithrocebus patas</i>		28.6	42.9	28.6	7	50		50	7	4
<i>Papio anubis</i>	25.8	75	25	0	4					5
<i>Cercopithecus aethiops</i>	31.5	20	80	0	5					6
<i>Pan paniscus</i>	23.2	17.6	64.7	5.9	15					7
<i>Pan troglodytes</i>	23.2	77.8	22.2	0	9					8
<i>Cebus apella</i>		100			1					9
<i>Leontopithecus</i>		44.4	44.4	11.1	9					10
<i>Alouatta palliata</i>	20.4	83.3	16.7	0	6	33.3	50	16.7	6	11
<i>Alouatta palliata</i>	20.4	100			1					12
<i>Alouatta caraya</i>		14.3	71.4	14.3	7	57.1	42.9	0	7	13
<i>Alouatta fusca</i>		100			1					14
<i>Alouatta seniculus</i>	35	23.5	41.2	35.3	17	6.7	80	13.3	15	15
<i>Alouatta seniculus</i>	35	57.1	28.6	14.3	7	66.7	33.3	0		16
<i>Brachyteles arachnoides</i>	8	100			1	100			1	17
<i>Ateles belzebuth</i>	4.4	40	60	0	10					18
<i>Ateles belzebuth</i>	4.4	42.9	28.6	28.6	14	16.7	75	8.3	12	16
<i>Lagothrix lagothricha</i>	6.75	50.0	43.8	6.3	16	33.3	44.4	22.2	9	16
Average		48.8	48.3	13.6		45.5	54.3	15.8		

^aReferences: (1) Overdorff and Strait (1998), (2) Dew and Wright (1998), (3) Scharfe and Schlund (1996), (4) Lieberman and Lieberman (1986), (5) Lieberman *et al.* (1979), (6) Foord *et al.* (1994), (7) Idani (1986), (8) Wrangham *et al.* (1994), (9) Padroni and Sanchez (1997), (10) Passos (1997), (11) Estrada and Coates-Estrada (1984), (12) Pruetz *et al.*, (1996), (13) Bravo (in preparation), (14) Estrada and Zunino (2000), (15) De Figueiredo (1993), (16) Julliot (1996), (17) This study (17) Moraes and Paoli (1995), (18) Nunes, (1998).

Note. Each cell indicates the percentage of plant species that showed higher, not significant (ns), or lower germination rates than control seeds, and the percentage of plant species in which dispersed seeds had a shorter, similar or longer latency periods than control seeds. Transit time of seeds in the digestive tract of some of the primate species is shown in the second column, per Lambert (1998).

or maintained germination rates similar to those of control seeds, and in very few cases they reduced germination success. Similarly, latency periods of primate-dispersed seeds are similar to, or shorter than those of control seeds, and the dispersal process rarely delays germination time (Table III).

Finally, it is important to note some additional problems in making interspecific comparisons, which are related to how control seeds are selected and treated. First, seed germination rates seem to be associated with the type of substrate used for experiments. For example, in our study the seeds placed on cotton tissue within petri dishes showed, on average, lower germination rates than seeds grown on soil. Second, selecting control seeds can

be subjective. It is very common for studies on germination rates to use hand-cleaned seeds as controls, but this procedure may ameliorate some positive effects of dispersal. Both theoretical and empirical studies have shown that the fleshy pulp surrounding the seeds that fall directly under the canopy may have deleterious effects due to predation, fungal diseases and competition (Augspurger, 1983; Clark and Clark, 1984; Connell, 1971; Janzen, 1970). Such effects are not taken into account in the typical control seeds. Thus, it is likely that, for many species, the seeds that are not removed from the parental tree—natural controls—have lower germination success than hand-cleaned control seeds (Pruetz *et al.*, 1996). Conversely, a potential bias of seeds collected under the crown of parental trees is that they may be the ones dropped by frugivores or discarded by the tree because of insect damage or unusual developmental patterns.

Another potential problem may be violating the statistical requirement of independence within samples. It is common, especially in the case of fruits with multiple seeds, e.g., *Ficus syconium*, to extract many control seeds from the same fruit, but it is possible that all seeds from the same fruit have a similar (not independent) genetic and developmental histories that could affect germination rates. It would be more appropriate to collect seeds from different fruits and, if possible, from under the crowns of different trees. We recommend taking into account these factors, i.e. substrate and seed source, in future studies concerning the effect of endozoochory on germination parameters, and using the appropriate controls according to the purpose of the study.

In conclusion, even though most seeds do not absolutely require gut passage to germinate (only one species in our trials does), this study demonstrates that ateline species, as well as other primates that swallow seeds, can affect seed germination. They usually induce increased (or do not affect) seed germination rates when compared to noningested seeds, and decrease (or do not affect) latency periods. In a few cases they reduce germination rates or increase the time for germination. In addition, different plant species are affected in different ways by the dispersal process, and these particularities need to be accounted for in understanding the population dynamics of different plant species. Seed swallowing primates are important to forest regeneration, given their general positive effects on seed dispersal quality. By the process of dispersal, they might increase the likelihood of reproductive success of many seed species. Given that these are the most abundant frugivores in this forest, their effects on regeneration are important. Because germination rates are just one component of seed dispersal effectiveness, studies on other aspects of dispersal efficiency are imperatively needed to confirm the effectiveness of primates as seed dispersers, for example, studies investigating the fate of dispersed and non-dispersed seeds.

APPENDIX

Fruit species most consumed by 3 ateline species at Tinigua National Park (Stevenson *et al.*, 2000a). The number of minutes feeding on fruits of each plant species is shown for each monkey species (LA = *L. lagotricha*, AT = *A. belzebuth*, AL = *A. seniculus*), that were observed over 2,496 h of continuous focal-animal sampling. Bold numbers indicate cases in which the seeds of the fruits consumed were predated by the primates. Italicised numbers indicate that the seeds could be both dispersed and predated under particular conditions. The plus sign indicates that consumption has been observed outside sampling periods. Fruit and seed size are indicated by their maximal dimension. The number of seeds per fruit is also shown (only one number of seeds is provided for monocarps and infrutescences. The latter are indicated by an asterisk). The relative density of fruiting trees is indicated as the number of trees in 12 phenological transects (No. Fr. Trees/5.6 km). Crop size per tree was estimated using the following categories: 0 = 1 – 10 fruits, 1 = 10 – 100, 2 = 100 – 1000, 3 = 1000 – 10000, 4 = 10000 – 100000 and 5 > 100000

Plant Species	Consumption time (min) by			Fruit size (mm)	No. of Seeds	seed size (mm)	No. Fr Trees/ 5.6 km	Crop size
	LA	AT	AL					
<i>Alibertia cf. hadrantha</i>	61	8	20	33–37	15–22	8–10	6	1
<i>Apeiba aspera</i>	56	26		50–80	50–	2–4	11	1
<i>Astrocaryum chambira</i>	7	109		60–80	1	45–60	9	1
<i>Brosimum alicastrum</i>	217	106	676	11–30	1	7–13	5	4
<i>Brosimum guianense</i>	134	23	19	20–30	1–3	5–8	4	3
<i>Brosimum lactescens</i>	28	153	7	13–18	1–3	5–8	1	3
<i>Brosimum utile</i>	22	18	148	12–20	1	6–10	<1	4
<i>Castilla ulei</i>	28	39	149	30–70	10–20	10–13	8	2
<i>Cecropia membranacea</i>	40	101	69	15–20*	>999*	1–2	9	1
<i>Cecropia sciadophylla</i>	38	155	10	10–20*	>999*	1–2	2	1
<i>Celtis schippii</i>	+	4	66	14–18	1	6–7	1	3
<i>Chrysophyllum lucentifolium</i>	45	4		45–55	4	27–30	<1	1
<i>Clarisia biflora</i>	55	+		18–28	1	15–20	<1	3
<i>Coccoloba coronata</i>	53	+	19	9–13	1	7–9	<1	3
<i>Coussapoa orthoneura</i>	±	137	136	4–10*	20–	1–2	1	4
<i>Crepidospermum rhoifolium</i>	125	66		20–25	1–2	12–15	15	2
<i>Dendropanax caucanus</i>	21	3	33	8–13	3–5	4–6	4	2
<i>Dialium guianensis</i>	65			14–20	1	6–8	1	3
<i>Duguetia quitarensis</i>	+	16		50–80*	50*	13–18	11	0
<i>Enterolobium schomburgkii</i>	90	71	+	30–50	5–10	8–11	2	2
<i>Eugenia nesiotica</i>	3	3		23–26	1–2	12–15	4	1
<i>Ficus americana</i>	153	163	161	5–13*	>50*	<1	<1	5
<i>Ficus andicola</i>	49	315	290	16–18*	>50*	<1	2	5
<i>Ficus insipida</i>	±		118	28–35*	>50*	1	1	4
<i>Ficus maxima</i>	±		137	25–40	>50*	1	2	3
<i>Ficus nymphaeifolia</i>	55	138	13	18–28	>50*	<1	<1	4
<i>Ficus schultesii</i>	+	99		25–45	>50*	1	<1	4
<i>Ficus sphenophylla</i>	80	58	154	5–8	>50*	<1	1	5
<i>Ficus trigona</i>	28		20	10–18	>50*	<1	<1	5
<i>Ficus trigonata maximiliana</i>	97			20–30	>50*	1	1	4
<i>Ficus yoponensis</i>	16	130	67	10–20	>50*	<1	<1	5
<i>Garcinia macrophylla</i>	131	33		50–80	4	25–30	5	1
<i>Genipa americana</i>	64		32	80–120	>50	10–14	<1	1
<i>Guatteria punctata</i>	28	34		8–13	1	6–9	3	4

Appendix (Continued)

Plant Species	Consumption time (min) by			Fruit size (mm)	No. of Seed	seeds size (mm)	No. Fr Trees/ 5.6 km	Crop size
	LA	AT	AL					
<i>Gustavia hexapetala</i>	954	405	100	50-60	6-12	15-18	44	2
<i>Heisteria nitida</i>	+	31		12-18	1	7-9	<1	3
<i>Helicostylis tomentosa</i>	25	4		20-30	10-20	6-8	<1	2
<i>Henriettella fissanthera</i>	81	+		3-5	>50	<1	3	5
<i>Henriettella sylvestris</i>	58	+		4-6	>50	<1	1	5
<i>Hieronima alchorneoides</i>	39	44		3-6	1	2	1	5
<i>Hymenaea courbaril</i>	49			120-	4-6	27-32	<1	1
<i>Inga alba</i>	83	67		100-	10-15	7-10	2	3
<i>Inga cylindrica</i>	11	2		150-	10-17	23-28	15	3
<i>Inga cf. acreana</i>	172	17	14	150-	10-15	14-18	2	2
<i>Inga cf. marginata</i>	3			80-130	10-12	7-10	5	2
<i>Inga edulis</i>	39	4	7	200-	10-15	13-15	3	2
<i>Inga tessmannii</i>	7	8	13	250-	15-20	17-28	2	1
<i>Inga thibaudiana</i>	6	4		120-	10-20	12-14	2	1
<i>Iriartea deltoidea</i>	5	44	4	28-40	1	20-25	12	2
<i>Jacaratia digitata</i>	67	53		110-	>50	3-6	1	1
<i>Laetia corymbulosa</i>	45			15-25	10-20	2-3	3	2
<i>Laetia procera</i>	2	75		6-18	30-50	2-3	<1	2
<i>Leonia glycyarpa</i>	54	73	11	35-70	15-25	14-18	4	2
<i>Malmea sp.</i>	44	+		40-50	1	15-20	1	2
<i>Neea laxa</i>	14	3		10-13	1	8-10	9	4
<i>Ocotea cf. oblonga</i>	±	24		14-16	1	12-14	<1	2
<i>Ocotea longifolia</i>	+	53		10-14	1	11-14	1	3
<i>Oenocarpus bataua</i>		494	28	40-50	1	30-40	35	2
<i>Oenocarpus mapora</i>		73		15-18	1	15-20	3	2
<i>Perebea xanthochyma</i>	24	9	5	12-20	1	9-12	4	3
<i>Pourouma bicolor</i>	183	184	27	13-18	1	8-17	3	4
<i>Pourouma minor</i>	15	11	120	15-25	1	13-18	<1	3
<i>Pourouma petiolulata</i>	31	43	60	13-18	1	9-14	3	4
<i>Pouteria reticulata</i>	+	27		23-30	1	15-20	<1	3
<i>Protium crenatum</i>	173	161	4	20-25	1-3	13-17	7	2
<i>Protium glabrescens</i>	92	142	5	20-25	1-2	13-17	25	3
<i>Protium robustum</i>	33	2		19-25	1-5	13-17	18	2
<i>Protium sagotianum</i>	55	36	18	25-30	1-5	14-20	15	2
<i>Pseudolmedia laevigata</i>	40	48	74	11-15	1	6-9	7	4
<i>Pseudolmedia laevis</i>	36	92	59	8-14	1	6-9	26	4
<i>Pseudolmedia obliqua</i>	37	85	226	20-25	1	12-14	2	4
<i>Sarcaulus brasiliensis</i>	117	323		20-25	1	15-20	1	3
<i>Simarouba amara</i>	34	9	13	14-18	1	12-16	<1	3
<i>Socratea exorrhiza</i>	39	78	+	30-35	1	15-25	18	2
<i>Spondias mombin</i>	715	157	22	25-35	1	20-25	1	3
<i>Spondias venulosa</i>	653	2		25-35	1	20-25	4	3
<i>Stryphnodendron guianense</i>	43			70-100	7-13	7-9	2	3
<i>Swartzia arborescens</i>			3	40-100	1-2	25-35	2	1
<i>Syagrus sancona</i>	13	46	15	32-35	1	28-32	4	2
<i>Tabebuia serratifolia</i>	+			200-	>50	28-40	<1	1
<i>Theobroma glaucum</i>	+			130-	30-60	20-25	8	0
<i>Trichilia verrucosa</i>	32	10		18-25	2-3	17-22	4	2

(Appendix *Continued*)

Plant Species	Consumption time (min) by			Fruit size (mm)	No. of Seed	seeds size (mm)	No. Fr Trees/ 5.6 km	Crop size
	LA	AT	AL					
<i>Trichilia pleeana</i>	+		25	10–17	1	7–9	2	3
<i>Trichilia tuberculata</i>	9	118		10–18	1–2	10–17	6	3
<i>Virola calophylla</i>	7	46		23–25	1	13–16	2	2
<i>Virola flexuosa</i>	15	360		17–20	1	11–14	1	3

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