



Effectiveness of Spider Monkeys (*Ateles geoffroyi vellerosus*) as Seed Dispersers in Continuous and Fragmented Rain Forests in Southern Mexico

Óscar M. Chaves · Kathryn E. Stoner ·
Víctor Arroyo-Rodríguez · Alejandro Estrada

Received: 8 December 2009 / Accepted: 24 May 2010
© Springer Science+Business Media, LLC 2010

Abstract Seed dispersal is considered a key process determining spatial structure and dynamics of plant populations, and has crucial implications for forest regeneration. We evaluated the effectiveness of spider monkeys (*Ateles geoffroyi*) as seed dispersers in continuous and fragmented habitats to test if this interaction is altered in forest fragments. We documented fruit and seed handling, defecation patterns, diversity and composition of seeds in feces, and seed germination of defecated and control seeds in the Lacandona rainforest, Mexico. For most species contributing to 80% of total fruit feeding time, monkeys swallowed and spat seeds, but swallowing was the most frequent seed handling category in continuous and fragmented forests. However, the proportion of feeding records of swallowed seeds was higher in continuous forest (0.59) than in fragments (0.46), whereas the opposite was true for proportion of dropped seeds (0.16 vs. 0.31). This pattern was reflected in the number of fecal samples containing seeds, which was greater in continuous (95.5%) than in fragmented forests (82.5%). Seeds in fecal samples included a total of 71 species from 23 plant families. The numbers of defecated seed species were similar between forest conditions, and in both cases most seeds (>86%) were undamaged. Defecated seeds showed greater germination percentages than control seeds in all of the five species evaluated. Although we identified some differences in

Electronic supplementary material The online version of this article (doi:10.1007/s10764-010-9460-0) contains supplementary material, which is available to authorized users.

Ó. M. Chaves (✉) · K. E. Stoner · V. Arroyo-Rodríguez
Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México (UNAM),
Antigua Carretera a Pátzcuaro No. 8701, Ex Hacienda de San José de la Huerta, 58190 Morelia,
Michoacán, Mexico
e-mail: ochaba@gmail.com

A. Estrada
Laboratorio de Primates, Instituto de Biología, Universidad Nacional Autónoma de México,
Apartado Postal 176, San Andrés Tuxtla, Veracruz, Mexico

seed handling and the percentage of feces with seeds between continuous forest and fragments, our results indicate that, in general terms, spider monkeys are effective seed dispersers in both forest conditions.

Keywords Forest regeneration · Fragmentation · Frugivorous primates · Seed dispersal

Introduction

Plant recruitment, distribution, and regeneration of tropical forest species largely depend on the effectiveness of animals as seed dispersers (Cordeiro *et al.* 2009). Disperser effectiveness is defined in terms of the contribution a disperser makes to the future reproduction of a plant or to plant fitness, and may be considered from the perspective of both the dispersal agents and the dispersed plants at a variety of scales from individuals to communities (Jordano and Schupp 2000; Schupp 1993).

From the plant perspective, seed dispersal effectiveness depends on 2 main components: 1) the quantity of dispersed seeds and 2) the quality of seed dispersal, i.e., the probability that seeds are deposited intact in sites with high prospects for establishment (Muller-Landau and Hardesty 2005; Schupp 1993). According to Schupp (1993), the first component is a function of the number of visits made to the plant by a disperser and the number of seeds dispersed per visit, which depends on the abundance of the disperser, its feeding behavior, the fruit/seed handling strategies, and the reliability of visitation. The second component is a function of the quality of treatment given a seed in the mouth and in the gut, i.e., percentage of handled seeds destroyed and percentage of germination of defecated seeds, and the quality of seed deposition, i.e., defecation pattern, predator pressures, and probability of establishment. In sum, both the quantity and quality of seed dispersal determine the final fate of a seed, and in turn, the relative impact dispersers have on plant community structure and composition (Jordano and Schupp 2000; Schupp 1993).

Seed dispersal effectiveness may be particularly critical in forest fragments, in which some fruit-eating animal species disappear, e.g., birds: Martensen *et al.* (2008); bats: Cosson *et al.* (1999); large birds and mammals: Melo *et al.* (2010); and primates: Arroyo-Rodríguez *et al.* (2008), affecting plant species diversity and vegetation structure (Moran *et al.* 2009). This threat is higher for large-seeded tree species because their dispersal agents are often large-bodied, and hence at greater risk of local extinction in fragments, i.e., with greater hunting pressures, lower reproductive rates, smaller population sizes, and in many cases, with larger home range requirements (Stoner *et al.* 2007). This is the case for primates, which constitute 25–40% of the frugivore biomass in tropical forests (Chapman 1995), and are important seed dispersers for many tree species (Link and Di Fiore 2006). Overall, ecological services provided by primates through seed dispersal are critical for the recruitment of many medium- and large-seeded plant species in both continuous and fragmented forests (Stevenson and Aldana 2008).

In Neotropical primates researchers have evaluated seed dispersal effectiveness only in a few species, and mainly in continuous forests, e.g., *Lagothrix lagotricha*: Stevenson (2000), *Alouatta seniculus*: Julliot (1996); and *Cebus capucinus*: Valenta

and Fedigan (2009). These studies have assessed only isolated aspects of dispersal effectiveness, e.g., dispersal distance and germination rates: Stevenson (2000), fruit choice: Stevenson (2004), and dispersal quantity: Link and Di Fiore (2006) and Stevenson (2007) and did not consider the potential effect of the site-specific vegetation structure, e.g., abundance and diversity of food species for primates, on the aspects evaluated. Thus, for a given primate species, observed patterns of seed dispersal may be more related to differences in intersite plant species composition and abundance, which result in differential fruit availability at each site, than only to differences in the behavior of the disperser among habitats, e.g., *Ateles* spp.: Russo *et al.* (2005). Despite these facts, evidence suggests that effectiveness of primates as seed dispersers is highly variable in terms of proportion of fruit in the diet, number of seed species in feces, size of swallowed seeds, percentage of fecal samples without seeds, and effect of gut passage on seed germination (Table SI). For example, fruit in the diet for some sympatric primates may range from 2% (*Alouatta seniculus*: Orihuela-López *et al.* 2005) to 87% (*Ateles belzebuth*: Dew 2008). The number of seed species in feces may range from 9 (*Alouatta palliata*: Wehncke *et al.* 2004) to 133 species (*Ateles belzebuth*: Link and Di Fiore 2006). Contrasting defecation patterns have been reported for different primates, e.g., scattered in *Cebus capucinus*: Wehncke *et al.* 2004; clumped in *Alouatta seniculus*: Andresen 2002), which may differentially affect the probability of seed and seedling survival (Howe 1989). Similarly, researchers have reported positive, neutral, and negative net effects of primate gut passage on seed germination; nevertheless, positive effects are more frequent (Table SI).

Postdispersal seed fate including the effect of secondary seed dispersers and predators, e.g., dung beetles and scatter hoarding rodents, represent additional elements influencing the effect of primary seed dispersers on plant fitness (Schupp and Fuentes 1995). Although most secondary dispersers move seeds short distances and frequently bury them close to the original deposition microsite, e.g., <1 m in dung beetles (Andresen 2002), the cached seeds often have a higher survival than the uncached seeds (Andresen and Levey 2004; Forget and Cuijpers 2008). However, secondary dispersal is less likely to occur when highly frugivorous and mobile primates, such as spider monkeys, are the primary seed dispersers than when they are not (Forget and Cuijpers 2008).

In continuous forests, evidence suggests that spider monkeys are legitimate seed dispersers for a large number of plant species because they swallow large quantities of seeds and defecate them intact (Di Fiore *et al.* 2008), and they transport seeds far away (>100 m) from parent trees to sites with higher probability of seedling establishment (Link and Di Fiore 2006). Nevertheless, no study to date has examined simultaneously different quantitative and qualitative aspects of *Ateles*' seed dispersal effectiveness and how these attributes are modified in forest fragments. In spite of this fact, evidence suggests that primate-plant interactions may be negatively affected in forest fragments because these habitats often present less availability of fruit resources for primates in comparison with continuous forests (Arroyo-Rodríguez and Mandujano 2006; Dunn *et al.* 2009), forcing frugivorous primates to adjust their feeding behavior, e.g., exploiting alternative plant items (González-Zamora *et al.* 2009; Onderdonk and Chapman 2000).

We aimed to determine the effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as primary seed dispersers in quantitative and qualitative terms and to assess if this interaction is altered in forest fragments. We estimated seed dispersal effectiveness in areas of continuous and fragmented forest in Lacandona, Chiapas, Mexico, by analyzing 1) seed handling of the top fruit plant species and its relationship with seed size; 2) defecation patterns; 3) diversity and composition of defecated seed species, and percentage of undamaged seeds; and 4) germination of defecated versus control seeds. Because spider monkeys are highly frugivorous and commonly defecated in a scattered pattern (Di Fiore *et al.* 2008; Howe 1989; Russo 2005) we predict that they will be effective seed dispersers in terms of number of defecated seeds, defecation pattern, and the effect of gut passage on the germination in continuous forest and fragments. However, because fruit availability is often reduced in forest fragments promoting shifts in primates' feeding behavior, we also predict that fragments will experience a decrease in the proportion of seeds ingested, the number of seed species defecated, and the proportion of feces with seeds. This is the first study that documents the importance of a Neotropical monkey on seed dispersal effectiveness in forest fragments (*cf.* González-Di Piero *et al.* [in press](#)).

Methods

Study Sites and Spider Monkey Communities

We studied the fruit-eating behavior of 6 communities of spider monkeys: 3 independent communities in 3 different areas of the Montes Azules Biosphere Reserve (MABR, >3000 km²) separated by ≥ 4 km, i.e., the closest distance among home range perimeters, and 3 communities in 3 different fragments located in the Marqués de Comillas Region (MCR), Chiapas, Mexico (for further details see [electronic supplementary material](#)). All fragments in MCR were isolated ≥ 24 yr ago, and their sizes were 14, 31, and 1125 ha (Table [SII](#)). For the 3 study sites of MABR and for the largest fragment, we restricted spider monkey follows to an area of 30–90 ha (depending on the movements of focal communities), whereas for the other 2 fragments we sample the entire area. Finally, although there are differences in size and distance among sites, both forest conditions—continuous forest and fragments—had a similar adult tree composition (see [electronic supplementary material](#)).

Primate Species in the Study Area

Two primate species are present in the study area: black-handed spider monkeys (*Ateles geoffroyi vellerosus*) and black howlers (*Alouatta pigra*). In MABR, the population density of *Ateles geoffroyi* has been estimated as 2.9 ind/km², while that for *Alouatta pigra* is 14.4 ind/km²; a gross estimate of these population densities in a large fragment at MCR is 9.3 and 13.3 ind/km², respectively (Estrada *et al.* 2004). Overall, howlers are characterized by having a folivorous diet (Di Fiore and Campbell 2007). By contrast, *Ateles* spp. has been described as a fruit specialist (Di Fiore *et al.* 2008) that accounts for >70% (ranging from 39% to 82%) of their feeding time (González-Zamora *et al.* 2009).

Feeding Behavior and Seed Handling

We studied the diet of spider monkeys during a 15-mo period (6 mo in the dry season: February–April 2007 and 2008; and 9 mo in rainy season: May–October 2007, and August–October 2008). We documented feeding behavior for each of the 6 focal communities during 3 consecutive days once every 3 wk, using 5-min focal animal sampling (Altmann 1974). We conducted follows from 0700 h to 1730 h, totaling 223 observation days and 1000 h of focal observations. Further details of feeding sampling are provided in the [electronic supplementary material](#).

We recorded the feeding behavior to determine how much of the diet was devoted to consumption of different plant items (Chaves *et al.* [in press](#)) but here we focus on the fruit diet. When monkeys were feeding on fruits we identified whether they were consuming ripe or unripe pulp/aril and we recorded growth-form (trees, shrubs, epiphytes, and climbers), species, and seed handling behavior. When we could not determine fruit development because of poor illumination, we simply recorded the food item as fruit. We calculated the relative importance of different fruit species in the diet as percent time spent consuming a particular fruit species in relation to total time feeding on fruits. We ranked the fruit species based on the percent of time spent consuming each fruit species in relation to the total time spent consuming all fruit species until the sum was 80% and recorded the seed handling only for these species (hereafter named top fruit species). We recognized three categories of seed handling: 1) swallowed—ingestion of the entire fruit swallowing pulp and seeds; 2) spat out—when monkeys ate the fruit pulp or aril and spat out the seeds under the parent tree while eating; and 3) dropped—when monkeys ingested only fruit pulp and dropped seeds under the parent tree. Finally, because the top fruit species were not the same in continuous forest and fragments, we restrict the statistical analysis to the 5 top fruit species present in both forest conditions —*Brosimum alicastrum*, *Ficus tecolutensis*, *Ficus* sp 1, *Spondias mombin*, and *S. radlkoferi*— to control for seed handling effects at the species level.

Defecation Pattern, Defecated Species, and Germination Trials

Following Wehncke *et al.* (2004), we classified deposition or defecation pattern as scattered, i.e., when monkeys defecated individually in space and time, creating a scatter of small defecations, or clumped, i.e., when a monkey community or subgroup defecated simultaneously in a particular place producing large areas of clumped defecations. In contrast to Russo and Augspurger (2004), we did not discriminate between sleeping sites and in-transit sites because in Lacandona the location of sleeping sites, both diurnal resting trees and nocturnal sleeping trees, varied over time. Further, we did not sample at dawn or dusk when the entire community was found together, but rather sampled from subgroups while foraging and moving throughout the day.

We collected fecal samples from individual monkeys immediately after defecation, and placed individually in labeled plastic bags and later processed in the field laboratory. We thoroughly rinsed each sample with water in a sieve using successively decreasing mesh size (3 mm and 1 mm mesh, respectively). The number, composition, and damage level of seed species in each sample was recorded

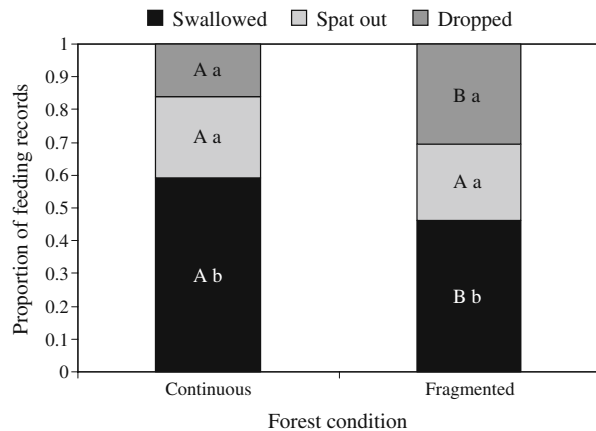
using a 14× triplet loupe magnifying lens. Seeds were classified as: 1) undamaged—intact seeds or with $\leq 5\%$ of the testa damaged; 2) moderate damage—seeds with $> 5\%$ to $\leq 25\%$ of the testa damaged; and 3) heavy damage— $> 25\%$ of the testa damaged. In both forest conditions, we ranked the defecated seed species based on the percent of fecal records containing each seed species in relation to the total fecal records for all seed species until the sum was 80% (hereafter named top defecated seed species). To identify seed species we used the Lacandona seed reference collection located at the Centro de Investigaciones en Ecosistemas (UNAM, Morelia, Mexico). Plant nomenclature followed the Missouri Botanical Garden nomenclatural update database (<http://mobot.org/W3T/search/vast.html>).

To examine the effect of seed passage through spider monkeys' digestive tracts, we performed a series of germination trials in 4 tree species —*Spondias radlkoferi*, *Ampelocera hottlei*, *Brosimum lactescens*, and *Faramea occidentalis*— and 1 vine —*Cissus verticillata*— with large seeds (1.4–4.5 cm in length). We selected these species because they represent important fruit sources for spider monkeys in the study area (comprising 6–40% of their fruit feeding time for the first 3 species and *ca.* 2% for the latter 2 species: Chaves *et al.* *in press*), and because their size limits potential dispersers to primates and a few large-bodied birds (Jordano 1995). We collected seeds for germination trials from fresh feces just after defecation and from mature fruits (control seeds). We collected mature fruits under the crowns of 5–14 parent trees where the monkeys fed. We manually removed pulp or aril and observed all seeds with a 14× triplet loupe magnifying lens to select only intact seeds, i.e., seeds without holes, malformations, or other damage to the testa. For each species, we used 14–40 seeds from 12–36 mature fruits (control seeds) and 15–30 seeds from 10–20 fecal samples. Defecated and control seeds were similar in size and weight and were collected from continuous forest. We placed seeds in 10×20 cm plastic boxes containing river sand and placed them in a green house (*ca.* 40% full sun) located in a 1-ha fragment at 150 m from MABR. We watered seeds daily for 12 wk and recorded germination, i.e., radicle emergence, daily.

Data Analysis

To evaluate if seed handling differed between continuous forest and fragments, we used generalized linear models (GLM: Crawley 1993). We estimated the proportion of records devoted to each category of seed handling per study site considering each of the 3 sites as replicates within each forest condition. As different seed handling occurs within each forest condition (Fig. 1), we nested seed handling within forest condition, with the whole model being: PROPORTION OF RECORDS = SEED HANDLING nested within FOREST CONDITION + SEED HANDLING*SPECIES nested within FOREST CONDITION + FOREST CONDITION. Proportion data were first arcsine transformed, and tested for a normal distribution with a Shapiro Wilk test (passed, $p > 0.1$). We then selected Normal distribution with an identity link-function to the response variable. To identify which seed handling categories were statistically different among each other, we used *post hoc* analyses with contrasts (Crawley 1993). We also explored the relationship between percentage of swallowed seeds and seed size in each forest condition with a linear regression of arcsine transformed proportions. To compare the defecation pattern in continuous and

Fig. 1 Seed handling in continuous and fragmented forest in Lacandona, Chiapas. Different capital letters indicate significant differences among forest conditions, and different lowercase letters indicate differences among seed handling categories within each habitat (contrast tests, $p < 0.05$).



fragmented forest we used a GLM, fixing a Poisson distribution and log-link function to the response variable, i.e., number of defecation records (Crawley 1993). Before analysis, we standardized the number of defecation records in each forest condition to control for differences in sample size. In addition, to test for consistency between fruit diet data obtained from foraging observations and defecated seeds, we estimated the species overlap between these 2 techniques via the Morisita-Horn index.

To test for differences in the number of defecated seed species per site and in the number of seed species per fecal sample between continuous and fragmented forests, we used analyses of deviance with GLM. As suggested for count response variables, we fixed a Poisson distribution to a log-link function (Crawley 1993). First, we standardized the number of fecal samples to control for differences in species density using the rarefaction approach (EcoSim: Gotelli and Entsminger 2001). We compared the number of fecal samples that contained no seeds via GLM, fixing a Poisson distribution and log-link function to the response variable. Finally, to compare the number of seeds that germinated from defecated vs. control seeds, we constructed a 2×2 contingency table for each species and tested differences via G -tests. We performed all statistical analyses using JMP (version 7.0, SAS Institute, Cary, NC).

Results

Feeding Behavior and Seed Handling

Overall, fruit made up $55.6 \pm 18.9\%$ (mean \pm SD) of the spider monkeys' diet ($57.0 \pm 27.1\%$ in continuous forest and $54.1 \pm 12.5\%$ in fragments). The monkeys consumed fruits from 73 species in continuous forest and 61 species in fragments. In general, for most top fruit species (*ca.* 90%), spider monkeys showed >1 category of seed handling, with swallowed being the most frequent category in both continuous (55.6% of species) and fragmented forests (60% of species; Table 1). The number of feeding records did not differ between forest conditions ($\chi^2 = 0.28$, $df = 1$, $p = 0.9$).

Table 1 Seed handling and seed size of top fruit species in the diet of *Ateles geoffroyi* communities inhabiting continuous forest and forest fragments in Lacandona, Chiapas

Forest condition/species	Family	Mean seed size (cm)	%TFT ^a	<i>n</i>	% Seed handling		
					Swallowed	Spat out	Dropped
Continuous forest							
<i>Spondias radlkoferi</i>	Anacardiaceae	3.87	33.1	661	10.4	37.4	47.0
<i>Ficus</i> sp 1	Moraceae	<0.1	10.3	27	100	0	0
<i>Spondias mombin</i>	Anacardiaceae	1.97	9.5	151	31.8	25.8	33.8
<i>Ficus tecolutensis</i>	Moraceae	<0.1	7.0	155	100	0	0
<i>Calatola laevigata</i>	Icacinaceae	1.20	5.6	35	100	0	0
<i>Ampelocera hottlei</i>	Ulmaceae	1.38	5.4	126	36.9	59.1	3.6
<i>Ficus obtusifolia</i>	Moraceae	<0.1	3.9	68	100	0	0
<i>Brosimum alicastrum</i>	Moraceae	1.58	3.4	85	14.2	61.2	24.6
<i>Inga punctata</i>	Fabaceae	1.32	2.1	27	75.9	24.1	0
Forest fragments							
<i>Spondias radlkoferi</i>	Anacardiaceae	3.87	20.5	358	7.1	32.5	59.6
<i>Brosimum alicastrum</i>	Moraceae	1.58	13.4	182	12.5	65	22.5
<i>Ficus tecolutensis</i>	Moraceae	<0.1	10.2	188	100	0	0
<i>Ficus</i> sp1	Moraceae	<0.1	9.3	194	99.0	1.0	0
<i>Dialium guianense</i>	Fabaceae	1.01	7.7	40	13.8	86.3	0
<i>Sabal mexicana</i>	Arecaceae	0.60	4.3	87	78.7	21.3	0
<i>Ficus</i> sp 2	Moraceae	<0.1	4.2	77	100	0	0
<i>Calatola laevigata</i>	Icacinaceae	1.20	4.0	40	100	0	0
<i>Spondias mombin</i>	Anacardiaceae	1.97	3.8	64	6.3	17.2	76.6
<i>Inga punctata</i>	Fabaceae	1.32	2.5	40	100	0	0

The number of seed handling records for each plant species is indicated (*n*). All species are trees with the exception of the palm *Sabal mexicana*.

^a Species were ranked based on the percent of time spent consuming each fruit species in relation to the total time spent consuming all fruit species until the sum was 80%.

However, it was significantly different among categories of seed handling nested within forest condition ($\chi^2=68$, $df=4$, $p<0.0001$), with the proportion of swallowed seeds being greater than spat out and dropped seeds in both forest conditions (contrast tests, $p<0.05$ in all cases; Fig. 1). The proportion of swallowed seeds was higher in continuous forest than in fragments (0.59 versus 0.46, contrast test: $p=0.01$), while the opposite was true for the proportion of dropped seeds (0.16 vs. 0.31, contrast test: $p=0.03$; Fig. 1). Further, we found significant differences among categories of seed handling by species nested within forest condition ($\chi^2=155$, $df=16$, $p<0.0001$), with seeds of *Spondias mombin* swallowed more in continuous forest than in fragments (mean \pm SD, $24\pm27\%$ and $5\pm4.5\%$ respectively; contrast test: $p=0.001$), while the opposite pattern occurred with the proportion of dropped seeds ($28\pm25\%$ and $73\pm6\%$ respectively; contrast test: $p<0.004$). We detected no other significant differences in the remaining 4 species (contrast tests: $p>0.05$ in all cases). Finally, the

percentage of seeds swallowed was inversely related to seed size in both continuous ($r=-0.84$, $p=0.005$) and fragmented forests ($r=-0.71$, $p=0.02$; Table I).

Defecation Pattern, Defecated Species, and Germination Trials

Scattered defecations were significantly more common than clumped defecations in continuous forest (94%, $n=523$) and fragments (89.4%, $n=496$, $\chi^2=912$, $df=2$, $p<0.0001$). However, the number of scattered and clumped defecations did not differ between forest conditions (contrast tests: $p=0.1$ in both cases).

We collected a total of 957 fecal samples (519 in continuous forest and 438 in fragments) and found seeds from 71 species (of which 52 were identified to species and 19 to morphospecies), 39 genera, and 23 families. The number of defecated seed species was similar between continuous forest (37 species and 9 morphospecies, range=18–27 species) and fragments (38 species and 13 morphospecies, range=18–24 species, $\chi^2=0.03$, $df=1$, $p=0.86$). Although species composition was similar between forest conditions (electronic supplementary material), only 21 out of 52 defecated seed species were shared between continuous forests and fragments, resulting in a moderate species overlap between forest conditions (Morisita-Horn's index=0.62).

The mean (\pm SD) number of seed species per fecal sample was 1.3 ± 0.8 species, ranging from 0 to 6 species, and we detected no significant differences between continuous forest and fragments (1.3 ± 0.8 and 1.3 ± 1.0 species, respectively; $\chi^2=0.64$, $df=1$, $p=0.42$). More than 90% of the fecal samples contained seeds, but the average percentage of feces without seeds was greater in fragments ($17.5\pm10\%$) than in continuous forest ($4.5\pm3.7\%$, $\chi^2=26.5$, $df=1$, $p<0.0001$). Finally, the overlap in the composition of fruit species in the diet based on direct observations from foraging data and seed species in feces was relatively high (Morisita-Horn's index=0.75), indicating that seeds collected from fecal samples reflect *ca.* 75% of what monkeys are feeding on.

In general, seed size in feces ranged from <0.1 cm in length and width (*Ficus* spp.) to *ca.* 4.2×2.3 cm in length and width, e.g., *Spondias radlkoferi* and *Attalea butyracea*. However, spider monkeys also ate the fruit pulp and dropped the seeds of *Licania platypus* (*ca.* 10×7 cm) in both forest conditions. Considering the top defecated seed species for all samples, spider monkeys defecated seeds of 12 species belonging to 9 genera and 7 families, with *Ficus* spp. (Moraceae) and *Spondias radlkoferi* (Anacardiaceae) being the most frequent in fecal samples (18.3% and 17.5% of fecal records, respectively). However, the number of species constituting the top defecated seed species was higher in fragments than in continuous forest (20 and 10 species, respectively; Table II). Seven out of 16 top defecated seed species were the same in both forest conditions (*Celtis iguanaea*, *Dialium guianense*, *Ficus tecolutensis*, *Ficus* sp 1, *Guarea glabra*, *Spondias radlkoferi*, and *S. mombin*; Table II). Of these species, *S. radlkoferi* and *F. tecolutensis* were the most frequent seed species in continuous forest, and *F. tecolutensis* and *Sabal mexicana* the most frequent in fragments. Overall, the percentage of undamaged seeds was $>86\%$ for most seed species in both forest conditions.

Finally, in the 5 studied species, the number of seeds that successfully germinated was significantly higher for defecated than for control seeds, indicating a positive effect in all cases (Table III).

Table II Top defecated seed species in communities of *Ateles geoffroyi* inhabiting continuous forest and forest fragments in Lacandona, Chiapas

Forest condition/ species	Family	Growth form	Number of fecal records	% Total fecal records ^a	<i>n</i>	% Undamaged seeds
Continuous forest						
<i>Spondias radlkoferi</i>	Anacardiaceae	Tree	187	26.8	579	100
<i>Ficus tecolutensis</i>	Moraceae	Tree	85	12.2	>23,300	–
<i>Cissus verticillata</i>	Vitaceae	Vine	57	8.2	250	100
<i>Spondias mombin</i>	Anacardiaceae	Tree	47	6.7	136	100
<i>Guarea glabra</i>	Meliaceae	Tree	40	5.7	142	100
<i>Ampelocera hottlei</i>	Ulmaceae	Tree	39	5.6	174	95.0
<i>Dialium guianense</i>	Fabaceae	Tree	39	5.6	202	97.5
<i>Celtis iguanaea</i>	Ulmaceae	Vine	29	4.2	216	100
<i>Paullinia costata</i>	Sapindaceae	Vine	18	2.6	59	100
<i>Ficus</i> sp 1	Moraceae	Tree	18	2.5	>2800	–
Fragmented forest						
<i>Ficus tecolutensis</i>	Moraceae	Tree	140	22.3	>58,800	–
<i>Sabal mexicana</i>	Arecaceae	Palm	50	8.0	293	100
<i>Dialium guianense</i>	Fabaceae	Tree	46	7.3	161	93.7
<i>Guarea glabra</i>	Meliaceae	Tree	46	7.3	120	100
<i>Ficus</i> sp 1	Moraceae	Tree	32	5.1	>4450	–
<i>Spondias radlkoferi</i>	Anacardiaceae	Tree	28	4.5	154	96.4
<i>Guarea grandifolia</i>	Meliaceae	Tree	26	4.2	93	100
<i>Inga</i> sp 1	Fabaceae	Tree	22	3.5	233	86.4
<i>Castilla elastica</i>	Moraceae	Tree	21	3.4	90	100
<i>Spondias mombin</i>	Anacardiaceae	Tree	19	3.0	77	100
<i>Acacia farnesiana</i>	Fabaceae	Shrub	14	2.2	64	92.3
<i>Ficus</i> sp 2	Moraceae	Tree	14	2.2	>2000	–
<i>Attalea butyracea</i>	Arecaceae	Palm	10	1.6	15	100
<i>Bactris balanoidea</i>	Arecaceae	Palm	8	1.3	16	100
<i>Inga</i> sp 2	Fabaceae	Tree	7	1.1	68	100
<i>Sapium</i> sp.	Euphorbiaceae	Tree	6	1.0	91	100
<i>Celtis iguanaea</i>	Ulmaceae	Vine	4	0.6	39	100
<i>Faramia occidentalis</i>	Rubiaceae	Shrub	4	0.6	27	100
<i>Ficus</i> sp 3	Moraceae	Tree	4	0.6	>300	–
<i>Nectandra</i> sp.	Lauraceae	Tree	4	0.6	23	100

– =undetermined data.

^a Species were ranked based on the percent of fecal records in which each seed species was found in relation to the total fecal records for all seed species until the sum was 80%.

Discussion

In concurrence with our first prediction, spider monkeys were effective seed dispersers in both quantitative and qualitative terms. In both continuous forest and

Table III Germination success of defecated versus control seeds

Plant species	% Germination				<i>G</i> -test	<i>p</i>	Effect
	Defecated	<i>n</i>	Control	<i>n</i>			
<i>Ampelocera hottlei</i>	33	15	6.6	15	7.93	0.005	+
<i>Brosimum lactescens</i>	100	15	29	14	23.9	0.0008	+
<i>Cissus verticillata</i>	55	20	6.2	16	10.8	0.001	+
<i>Faramaea occidentalis</i>	90	10	50	16	4.9	0.03	+
<i>S. radlkoferi</i>	38	24	2.5	40	14.6	0.001	+

Germination trials were 90 days except for *B. lactescens*, which was 20 days.

forest fragments they fed on a large number of fruit species and swallowed seeds of most of them, most feces contained seeds, a scattered deposition pattern was the most common, and the majority of defecated seeds were undamaged. Further, defecated seeds showed greater germination percentages than control seeds in all 5 plant species evaluated. Our results concur with previous studies on spider monkeys, which have shown that they are effective in terms of fruit diet diversity, seed handling, richness of seeds dispersed, and defecation pattern, e.g., *Ateles* spp.: Russo *et al.* (2005); *A. belzebuth*: Link and Di Fiore (2006), Dew (2008). Although we identified some differences in the seed handling and the percentage of feces with seeds between continuous forest and forest fragments, our study concurs with some recent studies showing that animal seed dispersal effectiveness is not notably affected by fragmentation, e.g., understory birds: Figueroa-Esquivel *et al.* (2009).

Seed Handling

Seed handling differed between forest conditions. Compared to communities in continuous forests, spider monkeys in fragments swallowed proportionally fewer seeds and dropped more seeds, which support our second prediction. Although we did not measure if seed handling is related to fruit shortage in fragments, there is some evidence that supports that fruit availability can be reduced in forest fragment (Arroyo-Rodríguez and Mandujano 2006). Although overall adult tree composition was similar in continuous and fragmented forests (electronic supplementary material), we found a greater abundance of larger trees (>60 cm in diameter at breast height [DBH]) of top fruit species in continuous forest compared to fragments (Fig. S2). Because the abundance of large trees is a good indicator of fruit availability (Chapman *et al.* 1992), it is likely that less fruit was available for spider monkeys in the studied fragments. Lower fruit availability often results in primates eating alternative plant items or more species, e.g., *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*: Chapman (1987); *Alouatta palliata*: Cristóbal-Azkarate and Arroyo-Rodríguez (2007). Indeed, this same pattern has been observed in our same studied monkeys. Chaves *et al.* (in press) found that spider monkeys in fragments invest proportionally more time consuming leaves and immature fruits than in continuous forest.

Because immature fruits are less palatable and contain more secondary metabolites than mature fruits (Waterman 1984), primates that eat immature fruits frequently drop or spit out more seeds (Norconk *et al.* 1998). We observed that spider monkeys feeding on immature fruits usually ate a small portion of the fruit pulp or aril and dropped or spat out the seeds directly under the parent tree. This is particularly the case for *Spondias radlkoferi* and *S. mombin*, in which spider monkeys dropped a higher proportion of seeds in fragments than in continuous forest. Exploiting more immature fruits in fragments may influence the seed dispersal effectiveness in 2 ways. First, seeds from immature fruits may have lower germination success owing to the presence of immature embryos and second, even if the seeds are viable and germinate, seeds dropped under parent trees commonly experience higher density-dependant mortality (Janzen 1970; Nathan and Casagrandi 2004). Finally, we found that the percentage of swallowed seeds decreased with seed size, which also has been reported in other primate studies, e.g., *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*: Chapman (1989); *Lagothrix lagotricha*: Stevenson *et al.* (2005).

One could speculate that because seed size of *Spondias* spp. is highly variable over years, habitats, individuals, and even within the same individual (Uribe Mú 2006), this fact may explain the differences we found in seed handling without invoking changes in handling behavior caused by fragmentation. However, it is reasonable to expect that variation in seed size should be present in all of our study species in both forest types, particularly in those with seeds >1 cm, owing to the high diversity of microhabitats in tropical forests, including access to light, water, and soil minerals (Allaby 2006). Based on this fact, we conclude that temporal and spatial differences in seed size of *Spondias* spp. are not sufficient to explain our results and that they are better explained by behavioral shifts in monkey communities inhabiting continuous forest and fragments.

Although from the individual's perspective, spitting out (or dropping) medium (0.5–1.5 cm in length) to large (>1.5 cm in length) seeds may be the most successful seed handling strategy, the ability of these primates to swallow large seeds certainly favors seed dispersal of large-seeded species in continuous and fragmented forests, e.g., *Attalea butyracea* and *Spondias* spp. However, this does not necessarily imply that spider monkeys are more effective dispersers for small than for large-seeded species, but rather the amount of swallowed seeds for each fruit species is negatively affected by their seed size owing to mechanical limitations related to fruit and seed handling (Jordano 1995). Further information about seed dispersal distance and seed fate is needed to clarify whether spider monkey seed dispersal effectiveness differs between seeds with contrasting sizes.

Defecation Pattern and Defecated Seed Assemblages

The effectiveness of primates as seed dispersers largely depends on the defecation pattern and diversity of seeds in feces. The higher the number of scattered depositions, seeds dispersed, and seed species in feces, the higher the probability of successful seed dispersal and seedling recruitment owing to a decrease in both the density and distance-dependent mortality near parents (Howe 1989; Muller-Landau and Hardesty 2005) and sibling competition for resources (Cheplick 1992; Queenborough *et al.* 2007). Although most defecations were scattered in both forest

conditions, the proportion of feces without seeds was significantly higher in fragments than in continuous forest, suggesting that some aspects of seed dispersal effectiveness may be negatively affected by fragmentation. In addition, the greater proportion of feces without seeds, as well as the higher number of species contributing to the top defecated seed species, is likely due to changes in foraging patterns in fragments.

Fecal samples contained seeds from 71 plant species (46 in continuous and 51 in fragments), indicating that spider monkeys provide seed dispersal services for many fleshy fruit species in both forest conditions. The number of defecated seed species was notably higher than that reported for spider monkeys in tropical dry forests (Chapman 1989) and for most *Alouatta* species in many tropical forests (Table SI); however, we found fewer plant species than those reported for some South American primates, e.g., *Alouatta seniculus*: Julliot (1996); *Ateles belzebuth*: Link and Di Fiore (2006); Table SI. This result can be explained by the higher plant species diversity in South America in comparison with Mesoamerica (Gentry 1982). Overall, dietary diversity in *Ateles* spp. is directly related with both proximity to the equator and mean annual rainfall (Di Fiore *et al.* 2008).

Despite the large number of seed species in feces, only a small number of species were abundant. This pattern is consistent with the selective foraging behavior characteristic of spider monkeys throughout their geographic range (Di Fiore *et al.* 2008; González-Zamora *et al.* 2009). In general, spider monkeys prefer to feed on species with large tree sizes, fleshy fruits, long fruiting periods, and clumped distributions (Di Fiore *et al.* 2008). Our results concur with 2 recent reviews (Di Fiore *et al.* 2008; González-Zamora *et al.* 2009), showing that plant families such as Moraceae, Fabaceae, and Anacardiaceae, and genera such as *Ficus*, *Brosimum*, *Spondias*, *Dialium*, and *Inga* are keystone species for spider monkeys.

Effects of Gut Passage

In the 5 plant species evaluated, seed germination was significantly higher in defecated than in control seeds. This finding illustrates the positive effect that spider monkeys have on seed germination, a finding similar to that observed in other Neotropical primates, e.g., *Alouatta*, *Cebus* and *Lagothrix* (Table SI). In addition, though some primates can negatively affect the germination of some plant species (Table SI), in our study *Ateles geoffroyi* did not affect negatively the germination for any of the species studied, suggesting that it may be a more effective seed disperser than some other highly frugivorous species. For example, negative gut passage effect on seed germination ranges from 5% in *Lagothrix lagotricha* (Stevenson *et al.* 2002) to 28.6% in *Ateles belzebuth* (Link and Di Fiore 2006).

Conclusions

Our findings clearly demonstrate that, at least for the aspects of effectiveness evaluated, spider monkeys are effective seed dispersers in both continuous forest and fragments. Dispersal services provided by spider monkeys in Lacandona may be especially important for large-seeded species such as *Ampelocera hottlei* and *Spondias* spp. (Chaves *et al. unpubl. data*), owing to the limited number of animals

that can swallow seeds of these large-seeded species (Stevenson and Aldana 2008). Although evidence suggests relationships among angiosperms and their animal dispersers are generally best described as diffuse networks rather than close coevolutionary relationships (Herrera 1985), services provided by legitimate dispersers, such as spider monkeys, undoubtedly may favor gene flow, and recruitment of their top food plant species (Schupp and Fuentes 1995; Stevenson *et al.* 2002). We recognize the limitations of our study that make it difficult to infer the effects of seed dispersal by these monkey communities on plant populations. For instance, we did not determine fruit availability in each study site, we did not provide a quantification of seed dispersal at the monkey population level, we restricted the germination tests to a small number of species, and we did not evaluate the final fate of defecated seeds. We suggest that more long-term studies quantifying seed dispersal by spider monkeys at the population level, as well as the final fate of defecated seeds, are critical to improve our understanding about the contribution of spider monkeys (and other Neotropical primates) to plant regeneration.

Acknowledgments This research was supported by grants from the Consejo Nacional de Ciencia y Tecnología, México (CONACyT Grant CB-2005-51043 and CB-2006-56799). This article constitutes a partial fulfillment of the Graduate Program in Biological Sciences of the National Autonomous University of México (UNAM). The organization Idea Wild provided equipment. This study would not have been possible without the collaboration of the local people in Loma Bonita, Chajul, Reforma Agraria, and Zamora Pico de Oro ejidos. V. Sork, D. Scofield, P. Thompson, and M. Quesada provided useful comments and suggestions in advanced drafts of this article. We thank C. Hauglustaine, C. Balderas, S. Martínez, J. Herrera, A. González-Di Pierro, and R. Lombera for field assistance. J. Rodríguez collaborated in the identification of seeds, and J. M. Lobato, G. Sánchez, H. Ferreira, and A. Valencia provided technical support. We also thank J. M. Setchell, E. W. Schupp, and 1 anonymous reviewer for valuable criticisms and suggestions that improved the manuscript.

References

- Allaby, M. (2006). *Tropical forests*. New York: Chelsea House Publishers.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behavior*, 49, 227–267.
- Andresen, E. (2002). Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica*, 34, 261–272.
- Andresen, E., & Levey, D. J. (2004). Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, 139, 45–54.
- Arroyo-Rodríguez, V., & Mandujano, S. (2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology*, 27, 1079–1096.
- Arroyo-Rodríguez, V., Mandujano, S., & Benítez-Malvido, J. (2008). Landscape attributes affecting patch occupancy by howler monkeys (*Alouatta palliata mexicana*) at Los tuxtlas, Mexico. *American Journal of Primatology*, 70, 69–77.
- Chapman, C. A. (1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica*, 49, 90–105.
- Chapman, C. A. (1989). Primate seed dispersal: the fate of dispersed seeds. *Biotropica*, 21, 148–154.
- Chapman, C. A. (1995). Primate seed dispersal: Coevolution and conservation implications. *Evolutionary Anthropology*, 4, 74–82.
- Chapman, C. A., Chapman, L. J., Wingham, R., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, 24, 527–531.
- Chaves, O. M., Stoner, K. E., & Arroyo-Rodríguez, V. (in press). Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. *Biotropica*.
- Cheplick, G. P. (1992). Sibling competition in plants. *Journal of Ecology*, 80, 567–575.
- Cordeiro, N. J., Indangalasi, H. J., McEntee, J. P., & Howe, H. F. (2009). Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology*, 90, 1030–1041.

- Cosson, J. F., Pons, J. M., & Masson, D. (1999). Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology*, 15, 515–534.
- Crawley, M. (1993). *GLIM for ecologists*. Oxford: Blackwell Scientific Publications.
- Cristóbal-Azkarate, J., & Arroyo-Rodríguez, V. (2007). Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: Effects of habitat fragmentation and implications for conservation. *American Journal of Primatology*, 69, 1013–1029.
- Dew, J. L. (2008). Spider monkeys as seed dispersers. In C. J. Campbell (Ed.), *Spider monkeys: Behavior, ecology and evolution of the genus Ateles* (pp. 155–182). Cambridge: Cambridge University Press.
- Di Fiore, A., & Campbell, C. J. (2007). The Atelines: variation in ecology, behavior, and social organization. In C. J. Campbell, A. Fuentes, K. C. Mackinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 155–185). Oxford: Oxford University Press.
- Di Fiore, A., Link, A., & Dew, J. L. (2008). Diets of wild spider monkeys. In C. J. Campbell (Ed.), *Spider monkeys: Behavior, ecology and evolution of the genus Ateles* (pp. 81–137). New York: Cambridge University Press.
- Dunn, J. C., Cristóbal-Azkarate, J., & Veà, J. J. (2009). Differences in diet and activity pattern between two groups of *Alouatta palliata* associated with the availability of big trees and fruit of top food taxa. *American Journal of Primatology*, 71, 654–662.
- Estrada, A., Van Belle, S., & García del Valle, Y. (2004). Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys along the Río Lacantún, Chiapas, Mexico. *Neotropical Primates*, 12, 70–75.
- Figuroa-Esquivel, E., Puebla-Olivares, F., Goudínez-Álvarez, H., & Núñez-Farfán, J. (2009). Seed dispersal effectiveness by understory birds on *Dendropanax arboreus* in a fragmented landscape. *Biodiversity and Conservation*, 18, 3357–3365.
- Forget, M., & Cuijpers, L. (2008). Survival and scatterhoarding of frugivores-dispersed seeds as a function of forest disturbance. *Biotropica*, 40, 380–385.
- Gentry, A. H. (1982). Neotropical floristic diversity: Phytogeographical connections between Central and South America, pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of Missouri Botanical Garden*, 69, 557–593.
- González-Di Pierro, A., Benítez-Malvido, J., Méndez, M., Zermeño, I., Arroyo-Rodríguez, V., Stoner, K. E., & Estrada, A. (in press). Effects of the physical environment and primate gut passage on the early establishment of *Ampelocera hottlei* Standley in tropical rainforest fragments. *Biotropica*
- González-Zamora, A., Arroyo-Rodríguez, V., Chaves, O. M., Sánchez-López, S., Stoner, K. E., & Riba-Hernández, P. (2009). Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: Current knowledge and future directions. *American Journal of Primatology*, 71, 8–20.
- Gotelli, N. J., & Entsminger, G. L. (2001). *EcoSim: Null models software for ecology*. Version 7.0. Acquired Intelligence Inc. & Kesey Bear. (<http://homepages.together.net/~gentsmin/ecosim.htm>).
- Herrera, C. (1985). Determinants of plant-animal coevolution: The case mutualistic vertebrate seed disperser systems. *Oikos*, 44, 132–41.
- Howe, H. F. (1989). Scatter and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia*, 79, 417–426.
- Janzen, D. H. (1970). Herbivores and the number of tree species in the tropical forest. *American Naturalist*, 104, 501–528.
- Jordano, P. (1995). Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist*, 145, 163–191.
- Jordano, P., & Schupp, E. W. (2000). Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, 70, 591–615.
- Julliot, C. (1996). Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *International Journal of Primatology*, 17, 239–258.
- Link, A., & Di Fiore, A. (2006). Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *Journal of Tropical Ecology*, 22, 235–246.
- Martensen, C. A., Pimentel, R. G., & Metzger, J. P. (2008). Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. *Biological Conservation*, 141, 2184–2192.
- Melo, F. P. L., Martínez-Salas, E., Benítez-Malvido, J., & Ceballos, G. (2010). Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. *Journal of Tropical Ecology*, 26, 35–43.
- Moran, C., Catterall, C. P., & Kanowski, J. (2009). Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biological Conservation*, 142, 541–552.

- Muller-Landau, H. C., & Hardesty, B. D. (2005). Seed dispersal of woody plants in tropical forests: Concepts, examples and future directions. In B. F. R. P. Burslem, M. A. Pinard, & S. E. Hartley (Eds.), *Biotic interactions in the tropics: Their role in the maintenance of species diversity* (pp. 267–309). Cambridge: Cambridge University Press.
- Nathan, R., & Casagrandi, R. (2004). A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *Journal of Ecology*, 92, 733–746.
- Norconk, M. A., Grafton, B. W., & Conklin-Brittain, N. L. (1998). Seed dispersal by neotropical seed predators. *American Journal of Primatology*, 45, 103–126.
- Onderdonk, D. A., & Chapman, C. A. (2000). Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology*, 21, 587–611.
- Orihuela-López, G., Terborgh, J., & Ceballos, N. (2005). Food selection by a hyperdense population of red howler monkeys (*Alouatta seniculus*). *Journal of Tropical Ecology*, 21, 445–450.
- Queenborough, S. A., Burslem, D. F. R. P., Garwood, N. C., & Valencia, R. (2007). Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology*, 88, 2248–2258.
- Russo, S. E. (2005). Linking seed fate to natural dispersal patterns: Factors affecting predation and scatterhoarding of *Virola calophylla* seeds in Peru. *Journal of Tropical Ecology*, 21, 243–253.
- Russo, S. E., & Augspurger, C. K. (2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecological Letters*, 7, 1058–1067.
- Russo, S. E., Campbell, C. J., Dew, J. L., Stevenson, P. R., & Suarez, S. A. (2005). A multi-forest comparison of dietary preferences and seed dispersal by *Ateles* spp. *International Journal of Primatology*, 26, 1017–1037.
- Schupp, E. W. (1993). Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, 107 (108), 15–29.
- Schupp, E. W., & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant-population ecology. *Ecoscience*, 2, 267–275.
- Stevenson, P. R. (2000). Seed dispersal by woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia: Dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology*, 50, 275–289.
- Stevenson, P. R. (2004). Fruit choice by woolly monkeys in Tinigua National Park, Colombia. *International Journal of Primatology*, 25, 367–381.
- Stevenson, P. R. (2007). Estimates of the number of seeds dispersed by a population of primates in a lowland forest in western Amazonia. In A. J. Dennis, E. W. Schupp, R. J. Green, & D. W. Westcott (Eds.), *Seed dispersal: Theory and its application in a changing world* (pp. 340–362). Wallingford, UK: CAB International.
- Stevenson, P. R., & Aldana, A. M. (2008). Potential effects of Ateline extinction and forest fragmentation on plant diversity and composition in the western Orinoco Basin, Colombia. *International Journal of Primatology*, 29, 365–377.
- Stevenson, P. R., Castellanos, M. C., Pizarro, J. C., & Garavito, M. (2002). Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia. *International Journal of Primatology*, 23, 1187–1204.
- Stevenson, P. R., Pineda, M., & Samper, T. (2005). Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagotricha*) at Tinigua Park, Colombia. *Oikos*, 110, 435–440.
- Stoner, K. E., Riba-Hernández, P., Vulinec, K., & Lambert, J. E. (2007). The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. *Biotropica*, 39, 316–327.
- Uribe Mú, C. A. (2006). Interacción entre el insecto barrenador *Oncideres albomarginata* Chamela y su planta hospedera *Spondias purpurea*. Ph.D. Thesis, Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México UNAM, Morelia, Michoacán, México.
- Valenta, K., & Fedigan, L. (2009). Effects of gut passage, feces, and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, 138, 486–492.
- Waterman, P. G. (1984). Food acquisition and processing as a function of plant chemistry. In D. J. Chivers, B. A. Wood, & A. Bilsborough (Eds.), *Food acquisition and processing in primates* (pp. 177–211). New York: Plenum Press.
- Wehncke, E. V., Valdez, C. N., & Domínguez, C. A. (2004). Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: Consequences for seed dispersal effectiveness. *Journal of Tropical Ecology*, 20, 535–543.