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Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity

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Abstract: Seed dispersal by frugivores is thought to play an important role in the maintenance of tropical forest diversity. Spider monkeys (*Ateles* spp.) are amongst the most frugivorous primates known, and they incorporate a diverse array of fruit species in their diets. In a 1-y study in lowland Ecuador, 670 h of focal observations and data on 916 faecal depositions were collected, and these data are used to describe the seed dispersal patterns of one group of wild spider monkeys (*Ateles belzebuth*) in terms of both the quantity of seeds dispersed and the primary seed shadows generated. Spider monkeys fed on the fruits of at least 152 plant species and swallowed seeds from more than 98% of these. Collected faecal samples contained seeds from at least 133 different plant species, with an average of 1.9 species (range: 0–7) per defecation. Individual spider monkeys dispersed a minimum of ∼195 000 seeds >1 mm in diameter per year, ∼35 000 of which were >3 mm in diameter. Mean retention time for seeds was 4.5 h. Seed dispersal distances averaged 443 m, but some seeds were moved >1250 m away from parental sources. These results suggest that declines in populations of spider monkeys might have a direct effect on forest dynamics, especially if other disperser species cannot compensate for their lost ecological services.

Key Words: *Ateles belzebuth*, dispersal distance, Ecuador, primates, retention time, seed dispersal, seed shadows, spider monkeys

INTRODUCTION

The redistribution of a plant's offspring through seed dispersal is thought to have a profound effect on the spatial distribution of tropical rain-forest plants and on the maintenance of tropical forest diversity (Harms *et al.* 2000, Jordano & Herrera 1995, Lambert & Garber 1998, Schupp & Fuentes 1995, Terborgh *et al.* 2002). Theoretical considerations of the importance of seed dispersal often focus on the role that animal dispersers play in moving seeds from parental tree crowns to locations where survival rates should be higher, according to classic ideas about density- and distance-dependent survival (Janzen 1970, Connell 1971). Although various studies have provided evidence of density-dependent effects acting at different life stages in some plant species (see Harms *et al.* 2000 and references therein), Harms *et al.* (2000) recently documented strong negative density-dependent recruitment from the seed to seedling stage for a large number of common plant species in a tropical forest on Barro Colorado Island, Panama. This large-scale study provides clear evidence that dispersal indeed increases the recruitment probability of seeds that are moved away from parental crowns (Hurtt & Pacala 1995, Schupp *et al.* 2002) and broadly supports the theoretical importance of seed dispersers for influencing forest diversity and dynamics (Howe & Miriti 2000).

Seed dispersal by animals is a ubiquitous process in tropical ecosystems, where between 50% and 90% of woody plant species are visited by vertebrate frugivores and most trees have fruits whose morphological features have apparently evolved to facilitate dispersal by animals (Fleming *et al.* 1987, Frankie *et al.* 1974, Gautier-Hion *et al.* 1985, Howe & Smallwood 1982, Janson 1983, Link & Stevenson 2004, Tabarelli & Peres 2002). Primate seed dispersers move large numbers of seeds from many different plant species (McConkey 2000, Poulsen *et al.* 2001, Stevenson 2000, Wrangham *et al.* 1994), and primary seed dispersal patterns have been described for a variety of primates (strepsirhines: Dew & Wright 1998; platyrrhines: Dew 2001, Garber 1986, Julliot 1996; Stevenson 2000, Wehncke *et al.* 2003, Zhang & Wang 1995; cercopithecoids: Lambert 1997, 1999; Rowell & Mitchell 1991; hominoids: McConkey 2000, Voysey *et al.* 1999a, b; Wrangham *et al.* 1994). Due to the suspected

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close interaction between plants and frugivores observed in a wide variety of ecosystems (McKey 1975, Ridley 1930, van der Pijl 1982), the study of animal-generated patterns of seed dispersal is key for understanding survival, recruitment, and population dynamics of tropical forest trees, as well as for the maintenance of tropical forest diversity (Cain *et al.* 2000, Schupp *et al.* 2002, Wang & Smith 2002, Webb & Peart 2001).

Throughout the Neotropics, spider monkeys (*Ateles* spp.) appear to be important seed dispersers as they (1) swallow and disperse large numbers of seeds from a diverse array of plant species, including a number of large-seeded taxa not ingested by most frugivores (Klein & Klein 1977, van Roosmalen 1985, Link, unpublished data), (2) can carry large numbers of seeds in their guts (Link & de Luna 2004, Peres 1994), (3) prey upon the seeds of very few plant species (Suarez 2003, van Roosmalen 1985), (4) have long daily travel distances and large home ranges (Klein & Klein 1977, Shimooka 2005, Suarez 2003), and (5) comprise a large proportion of the vertebrate frugivore biomass in many Neotropical lowland forests (Eisenberg *et al.* 1979, Glanz 1990, Terborgh 1983). Thus far, however, relatively few studies have attempted to describe the seed shadows generated by spider monkeys or to quantify their ecological role (but see Chapman 1989, Dew 2001, Russo 2003, Russo & Augspurger 2004). Here, we describe the pattern of seed dispersal created by one population of spider monkeys in a western Amazonian tropical rain forest. Specifically, we document the diversity of plant species dispersed, the number of seeds dispersed, and how seeds of various species are handled by spider monkeys. We also characterize spider monkeys' dispersal distances and retention times, examine the daily timing of seed depositions in relation to activity patterns, and discuss how unique aspects of the foraging and social strategies of spider monkeys may influence their seed dispersal patterns. Finally, we consider the significance of spider monkeys and other ateline primates in influencing the dissemination and spatial distribution of seeds at the landscape level and for understanding the dynamics of Neotropical forests.

Spider monkeys are some of the most vulnerable primates to habitat destruction, fragmentation, and hunting (Defler *et al.* 2003, Peres 1990, 2000, 2001; Peres & Dolman 2000, Stevenson *et al.* 2005), and all of these impacts have potentially disruptive implications for ecological processes in tropical forest (Chapman 1995, Chapman & Chapman 1995, Chapman & Onderdonk 1998, Peres & van Roosmalen 2002). As populations of spider monkeys decline, the ecological role that these primates play in dispersing seeds is likely to be altered (Chapman 1995, Lambert & Chapman 2005, Peres & van Roosmalen 2002), especially if other seed dispersers are not able to compensate for their lost ecological services (Peres & Dolman 2000, Stevenson *et al.* 2005).

METHODS

Study area and species

This study took place in the Proyecto Primates Research Area (75°28′W, 0°42′S), located south of the Río Napo, in Yasuní National Park, Ecuador. The study site covers an area of approximately 500 ha of primary terra firme forest dissected by several permanent streams. Mean annual rainfall is ~3200 mm, and, although rainfall is variable throughout the year, no month typically receives less than 100 mm. Mean annual temperature is ~26 °C and is relatively constant throughout the year. Additional information on the Proyecto Primates site has been reported by Di Fiore & Rodman (2001). The study site hosts at least 10 sympatric primate species, including three atelines (*Ateles belzebuth*, *Lagothrix poeppigii* and *Alouatta seniculus*), as well as a very diverse plant and animal community.

In Yasuní National Park, *Ateles belzebuth* is the largest primate, weighing approximately 8.5 kg (Franzen 2005). Its diet is composed primarily of fruits, supplemented with leaves, flowers and other minor items (Dew 2001, Suarez 2003, Link & Di Fiore, unpubl. data). Our study focused on a well-habituated group of 22 spider monkeys, comprising five adult males, nine adult females, three subadult females, three juveniles, and two infants that were born during the study. All individuals in the group were individually identifiable. Data on seed dispersal were only collected for adults and subadults.

Feeding and ranging data

We studied spider monkeys from September 2002 through August 2003 using continuous focal-animal follows (Altmann 1974). During follows, we tried to keep with the same focal individual as long as possible to determine seed passage times and dispersal distances. The first animal encountered on any given day was chosen as the initial focal subject and was followed either until the end of the day or until it was lost, at which point we switched to the next animal contacted as a new focal individual. In total, we collected 670 h of focal observation from all adult and subadult group members (5 males and 12 females). Our samples ranged in length from 0.5 to 12.5 h during the same day (average: 7 h 53 min ± 3 h 46 min SD, N = 85 follows). While our sampling regime could not be perfectly balanced across individuals given the difficulty of finding and following specific animals, we nonetheless collected a total of 134 h of focal observations (and data on 164 defecations) from males and just over 531 h of observation (and data on 590 defecations) from females, which is roughly equivalent to the proportional representation of the sexes in the group.

Moreover, for the 553 defecations that could be assigned to specific individuals, 142 (or an average of ~28 per focal individual) come from males and 411 (or an average of ~34 per focal individual) come from females, with only one male and two females from the group contributing fewer than 10 defecations to the dataset.

During focal follows, we recorded the position of the focal animal every 5 min in reference to a system of ~45 km of mapped trails marked every 25 m and more than 3000 mapped feeding sources that woolly monkeys and spider monkeys used during the present and previous studies (Di Fiore 1997, Suarez 2003). Animal locations and defecation sites were entered into a geographic information system, which was then used to estimate travel distances and paths. We estimated the group's home range as the minimum convex polygon of all the locations that we recorded throughout the year for the set of focal animals studied.

We also recorded the duration of all of the focal animal's feeding bouts, the type of item eaten (e.g. ripe fruits, young leaves), the taxonomic identity of the feeding source (following the nomenclature used in the Missouri Botanical Garden's VAST database: http://mobot.mobot.org/W3T/Search/vast.html), and whether seeds were swallowed, spat, or preyed upon when handled. In addition, we mapped the location of all trees fed in throughout the study, and we measured the diameter at breast height (dbh) and visually estimated the crop size of all major feeding patches (defined as those in which the focal animal fed for more than 5 min) following previously used methods (Di Fiore 1997, Di Fiore & Rodman 2001). Finally, whenever possible, fruits eaten by spider monkeys were collected to measure fruit and seed dimensions and weight.

Faecal samples and analysis

We collected as many faecal samples from the focal animals as possible and recorded the time and exact location of all their depositions. Nevertheless, faecal samples could not always be collected without interrupting continuous observation on the focal animals. Faecal samples from other individuals ranging in the same subgroup as the focal animal were also collected opportunistically. Samples from the same individual that were defecated in a period of less than 3 min were grouped into a single sample for analysis. We collected as many seeds as possible from each defecation, but not all seeds passed could be recovered as many of them do not reach the forest floor or because we were unable to find them in the dense vegetation. Although the number of faecal samples collected varied across months, the dataset includes samples from all months of the study except April 2003.

Each faecal sample was independently washed, and seeds that were retained with a 1-mm sieve were identified, counted, and measured. Following Stevenson (2000), we counted all individual seeds greater than 3 mm in their maximum dimension, while we grouped those with a maximum dimension of between 1 and 3 mm into three abundance categories: 20–50 seeds, 50–200 seeds and >200 seeds, and then used the lower bound of each categories in our analyses. Seeds were identified with the help of several expert botanists familiar with the flora of Yasuní National Park. For comparability to the largest number of published studies, we calculated estimates of the quantity of seeds dispersed based on both the mean and the median number of seeds recovered per defecation.

Dispersal distances and retention times

Defecated seeds that could be assigned to specific parental feeding patches were used as markers to estimate spider monkeys' gut passage times and dispersal distances. To obtain these data, several criteria had to be met that together reduce the probability of incorrectly assigning a defecated seed to a feeding patch different from its original source. Our criteria followed those of Stevenson (2000) and Russo (2003) and include the following: (1) the focal animal was followed continuously for an extended period without losing sight of it, (2) the focal animal fed from only one individual patch of the species assigned to a defecated seed during the sampling period (for dispersal distance estimates, the focal animal could feed on the same individual feeding patch several times, but not in other patches of the same species), and (3) seeds from that species were defecated for the first time at least 4.5 h after the beginning of sampling. This last criterion is designed to minimize the likelihood of inappropriately assigning a source to seeds swallowed before the onset of a sampling period. We based our last criterion on studies of captive spider monkeys (Milton 1981), in which the average retention time for seeds was just over 4 h, and ours is even more conservative than the 3.5-h criterion used by Russo (2003) as the minimum follow length used for estimating dispersal distances in another wild population of spider monkeys.

Out of the ~1400 potential cases in which at least one seed of a plant species was found in a faecal sample (estimated by multiplying the number of faecal samples collected, 738, by the average number of species of seeds found per sample, 1.9), we were able to estimate dispersal distances for 186 cases and retention times for 157 cases. As we did not follow focal animals over successive days and as we were unable to recover all seeds dispersed, our estimation of average retention time is likely to be an underestimate. Nonetheless, the average duration of those focal follows from which we successfully obtained retention time or dispersal distance data was 8.5 ± 2.5 h SD (range: 4.5–12.3 h, N = 31), and we presume that any error in our estimates of retention times would be minor given that in captive spider monkeys, the bulk of seeds pass through the digestive tract in less than 8 h (Milton 1981).

Temporal pattern of seed dispersal

To assess temporal patterns of defecation across the day, we grouped the number of defecations recorded during each hour and examined these as a function of sampling effort during those hours. We also looked at defecation patterns in relation to daily activity patterns, particularly with respect to resting periods. Specifically, we tested the idea that spider monkeys might advantageously adapt their defecation patterns to their feeding, foraging and resting strategies to avoid the energetic cost of carrying a ballast of non-nutritional seeds in their guts during travelling.

RESULTS

Diet and fruit handling

Spider monkeys consumed at least 152 fruit species during this study, and, in a previous study, Suarez (2003) reported that this same group ate from 238 fruit species. Our results thus reaffirm the high diversity of fruits in the spider monkey diet in Yasuní National Park. We found that spider monkeys swallowed seeds from almost all of the species from which they ate ripe fruits. Spider monkeys destroyed the seeds of only a few species of plants (e.g. *Astrocaryum chambira*, *Iriartea deltoidea*, *Socratea exorrhiza* and *Pseudolmedia laevis*), and these represented only 0.4% of the monkeys' feeding time and only 0.9% of their feeding bouts. Additionally, for only two species (the palms *Iriartea deltoidea* and *Socratea exorrhiza*) did we observe spider monkeys dropping most of the seeds from ripe fruits under parents rather than swallowing them.

Data on the time and location of deposition were collected for a total of 916 defecations, and we were able to collect faeces from 738 of these defecations. We recorded 133 species of seeds in these samples, and the fact that some species observed to be part of the spider monkeys' diet were not recovered in faecal samples is probably explained by insufficient sampling. The size of swallowed and defecated seeds ranged from ≤1 mm (e.g. *Ficus* sp.) to as large as 39 mm in maximum dimension (e.g. *Pouteria* sp.).

Dispersal quantity

Of the 916 defecations whose time and location we recorded, 664 were noted for the focal animal during follows, while 252 were recorded for other spider monkeys travelling in the same subgroup. Based on the focal data alone, spider monkeys defecated an average of 13.7 times per 12 h, excluding night hours when they were not observed. Throughout the year, faecal samples contained seeds from an average of 1.9 ± 1.3 SD different species (range: 0–7; N = 738), but this varied seasonally as dietary diversity varied between months (Link & Di Fiore, unpublished data). Only one sample was found without any seeds in it, and 77% of all faecal samples contained seeds from either 1 or 2 species of plant.

The faecal samples analysed contained an estimated 28 833 seeds >1 mm in maximum dimension, and we counted 5458 seeds >3 mm. Individual defecations contained a mean of 39.1 ± 69.9 SD seeds >1 mm (median: 7, range: 0–402) and 7.8 ± 8.9 SD seeds > 3 mm (median: 5, range: 1–74). Seeds >3 mm were present in 95% of defecations (700 out of 738 samples). However, of these, 80% (N = 561) contained fewer than 10 seeds in this size range, suggesting that while most defecations contained large seeds, relatively few of these seeds were deposited in any one location.

Using the mean value for the number of seeds passed per defecation, we estimated that individual spider monkeys dispersed an average of ∼536 seeds >1 mm per day (13.7 defecations per day multiplied by the mean of 39.1 seeds per defecation) and ∼107 seeds >3 mm per day. Based on these values and given that our group had a home range of 246 ha, we estimated that each non-juvenile spider monkey would disperse, on average, ∼795 seeds >1 mm ha^{-1} y^{-1} across the community home range, or ∼159 seeds >3 mm ha^{-1} y^{-1}. Together, the 17 non-juvenile members of our group dispersed an estimated ∼13512 seeds >1 mm ha^{-1} y^{-1}, or ∼2695 seeds >3 mm ha^{-1} y^{-1}. If the median number of seeds per defecation is used rather than the mean, all of these estimates would be somewhat lower (e.g. ∼142 seeds >1 mm, or ∼102 seeds >3 mm ha^{-1} y^{-1} dispersed by each non-juvenile animal). We found no significant differences between males and females in the either number of seeds >1 mm (Mann–Whitney U = 27100, P = 0.30, N = 583) or >3 mm (Mann–Whitney U = 23700, P = 0.24, N = 550) contained in depositions.

Seed damage, retention times and dispersal distances

Out of the 5458 seeds >3 mm passed, we found physical damage only on six of them, and in all cases this damage was caused by pre-dispersal predators, as evidenced by insect larvae that were found within the seeds.

We were able to estimate retention times for seeds belonging to 38 of 133 plant species (Table 1). The mean duration of seeds passing through the digestive tract was 4 h 29 min ± 1 h 34 min SD (range: 1 h 37 min–9 h

Table 1. Plant species whose seeds are swallowed by wild spider monkeys in Yasuní National Park, Ecuador and for which retention times and/or dispersal distances could be estimated.

			Retention time			Dispersal distance	
Family	Species	Days[a]	First appearance (min)	Average ± SD (min)	N	Average ± SD (m)	N
Anacardiaceae	*Spondias mombin*	1	158	158	1	30	1
	Tapirira guianensis	3	156	243 ± 105	11	264 ± 232	18
Annonaceae	*Guatteria* sp.	1	220	220	1	865	1
	Porcelia sp.	2	150	214 ± 90	4	246 ± 41	4
	Pseudomalmea diclina	2	207	259 ± 39	8	167 ± 103	8
	Rollinia cf. *helosioides*	1	279	279	1	1024	1
	Rollinia pittieri	1	204	277 ± 103	2	735 ± 224	2
Bombacaceae	*Matisia cordata*	1	177	275 ± 115	3	88 ± 4	3
Convolvulaceae	*Dicranostyles ampla*	1	ND	ND	0	130 ± 37	4
Cucurbitaceae	*Cayaponia* sp.	1	374	374	1	781	1
Euphorbiaceae	*Hyeronima alchorneoides*	1	166	196 ± 42	2	443 ± 144	2
Fabaceae	*Inga oerstediana*	1	226	226	1	257	1
	Inga sp. 2	1	152	152	1	416	1
Lauraceae	Lauraceae sp. 1	1	ND	ND	0	0	2
Meliaceae	*Guarea kunthiana*	1	277	343 ± 71	4	795 ± 96	4
	Guarea purusana	1	204	204	1	108	1
	Guarea sp.	1	214	214	1	303	1
	Trichilia laxipaniculata	1	192	205 ± 18	2	166 ± 72	5
	Trichilia sp.	1	236	261 ± 18	4	206 ± 0	4
Menispermaceae	*Abuta* sp.	1	246	338 ± 123	6	1060 ± 175	6
Moraceae	*Batocarpus* sp.	1	ND	ND	0	257 ± 138	8
	Clarisia racemosa	2	151	172 ± 26	3	264 ± 77	3
	Ficus sp.	1	98	164 ± 37	5	313 ± 11	5
	Naucleopsis glabra	1	220	311 ± 59	9	1183 ± 10	9
	Naucleopsis ulei	1	271	271	1	898	1
	Perebea xanthochyma	1	170	253 ± 56	4	907 ± 9	4
Myristicaceae	*Virola flexuosa*	1	171	171	1	293	1
	Virola obovata	1	118	246 ± 95	7	329 ± 159	7
	Virola pavonis	6	163	271 ± 83	14	435 ± 257	14
Myrtaceae	*Eugenia* sp.	2	296	447 ± 129	5	337 ± 69	5
Nyctaginaceae	*Neea* sp.	1	264	302 ± 53	2	1264 ± 25	2
Rhamnaceae	*Ziziphus cinnamomum*	2	163	272 ± 97	3	748 ± 415	3
Rosaceae	*Prunus debilis*	1	269	421 ± 132	3	585 ± 213	3
Rubiaceae	*Alibertia hadrantha*	1	97	236 ± 116	7	425 ± 152	7
Sapindaceae	*Cupania* sp.	1	157	299 ± 136	6	232 ± 146	9
	Talisia novagranata	1	186	343 ± 136	3	628 ± 196	3
Sapotaceae	Sapotaceae sp. 1	1	223	223	1	216	1
	Sapotaceae sp. 2	1	184	207 ± 32	3	121 ± 7	3
Ulmaceae	*Cissus* cf. *biformifolia*	4	208	292 ± 66	14	559 ± 255	14
	Cissus sp.	2	168	279 ± 105	3	189 ± 226	3
Verbenaceae	*Vitex* sp.	2	138	275 ± 94	9	466 ± 302	11

ND indicates "no data" available for a given cell.
[a] Number of distinct sampling days for which retention times or dispersal distances for the indicated species could be determined.

51 min, N = 157). The mean retention time increases somewhat to 5 h 12 min ± 1 h 43 min SD (N = 62) if the analysis is based only on focal samples lasting longer than 10 h. More than 80% of seeds were defecated between 3 and 7 h after being ingested (Figure 1), although we caution that there might be a bias against detecting longer retention times as focal animals were not followed across consecutive days. The average time to first appearance of seeds was 3 h 30 min ± 1 h 4 min SD (range: 1 h 37 min–6 h 17 min, N = 55).

The vast majority (85.4% or 159 out of 186) of seeds defecated by spider monkeys were deposited >100 m away from parental feeding patches. Only 11 seeds (5.9%) were deposited less than 50 m from parents and only four seeds (2.1%) were defecated within 20 m. These cases were associated with the rare instances where spider monkeys fed repeatedly on the same feeding patches before and just after a resting period, or when they spent long periods at a salt lick or at a dead tree where they ate large quantities of decayed wood (Suarez 2003, Link &

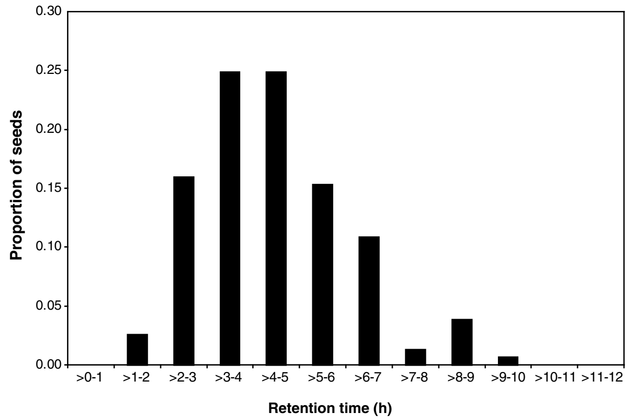

Figure 1. Distribution of seed retention times for wild spider monkeys in Yasuní National Park, Ecuador, based on 157 cases where seeds found in a faecal sample could be assigned to a specific parental plant.

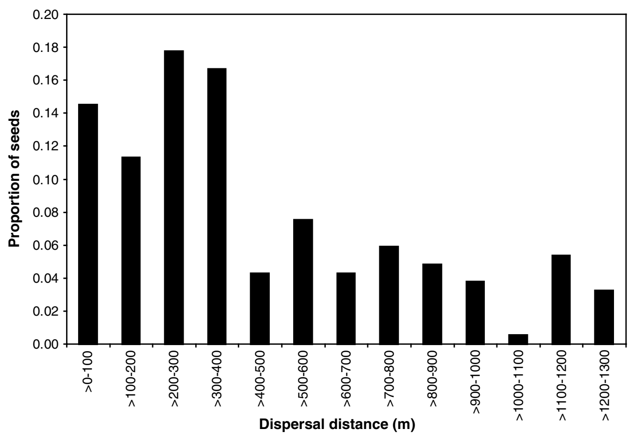

Figure 2. Distribution of seed dispersal distances for wild spider monkeys in Yasuní National Park, Ecuador, based on 186 cases where seeds found in a faecal sample could be assigned to a specific parental plant.

Di Fiore, unpublished data). The average dispersal distance for seeds was 443 m ± 334 m SD, although some seeds were dispersed up to 1281 m from their original source. If only those focal follows lasting more than 10 h are used, our estimate of average dispersal distance increases slightly to 490 m ± 333 m SD. Almost 60% of seeds were dispersed between 50 m and 450 m, with a median of 318 m (Figure 2).

For seeds dispersed on the same day of consumption, we found a weak but significantly positive correlation between dispersal distance and retention time, although the explanatory power of this correlation is low ($R^2 = 0.100$, $P < 0.001$, $N = 157$), and there is much scatter in the relationship. However, inclusion of dispersal distances for seeds swallowed and defecated on different days would tend to weaken this already weak correlation as spider monkeys seldom move during the night and often revisit the same feeding patch on successive days (see Stevenson 2000 for similar patterns in woolly monkeys).

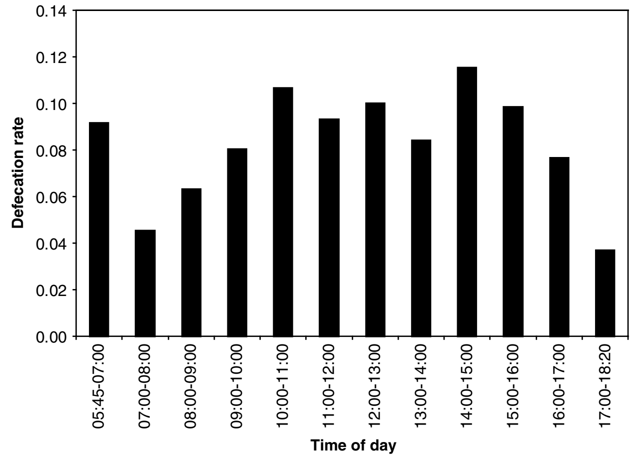

Figure 3. Defecation rates at different hours of the day. Bar values represent the total number of faecal samples divided by the total number of 5-min instantaneous sample points taken during the indicated time window over the course of the study.

Temporal pattern of defecations

Spider monkeys defecated throughout their daily activity period (05h45–18h20). Nevertheless, there was some clear diurnal patterning to defecations (Figure 3). First, spider monkeys had a higher defecation rate in the early morning, just before starting to move from their sleeping sites. In fact, the high rate noted between 05h45 and 06h15 is likely to be underestimated as collection of samples was difficult at this time of the day because there was little light in the understorey making visibility difficult. Although spider monkeys have been observed defecating at night (Link, pers. obs.; see also Russo 2003), a large proportion of the seeds that spider monkeys carry to their sleeping sites are probably defecated at dawn. After daily activities start, there is a period of about 2 h (06h15–08h30) where the rate of defecation is relatively low. During this time, spider monkeys generally eat extensively and then enter a first resting period. For the remainder of the day (08h30–16h30), the defecation rate increases as periods of travelling, eating, and resting characterize their activity. Finally, at the end of the day (16h30–18h20), there is another drop in the rate of defecation, probably as spider monkeys optimize the amount of food in their digestive system before extended periods of resting at their sleeping sites.

Spider monkeys appeared to regulate their defecation patterns according to their feeding and digestive cycles. Out of 655 defecations with associated time and location data recorded for focal animals, 42% occurred during resting, 40% while moving and 18% during feeding bouts.

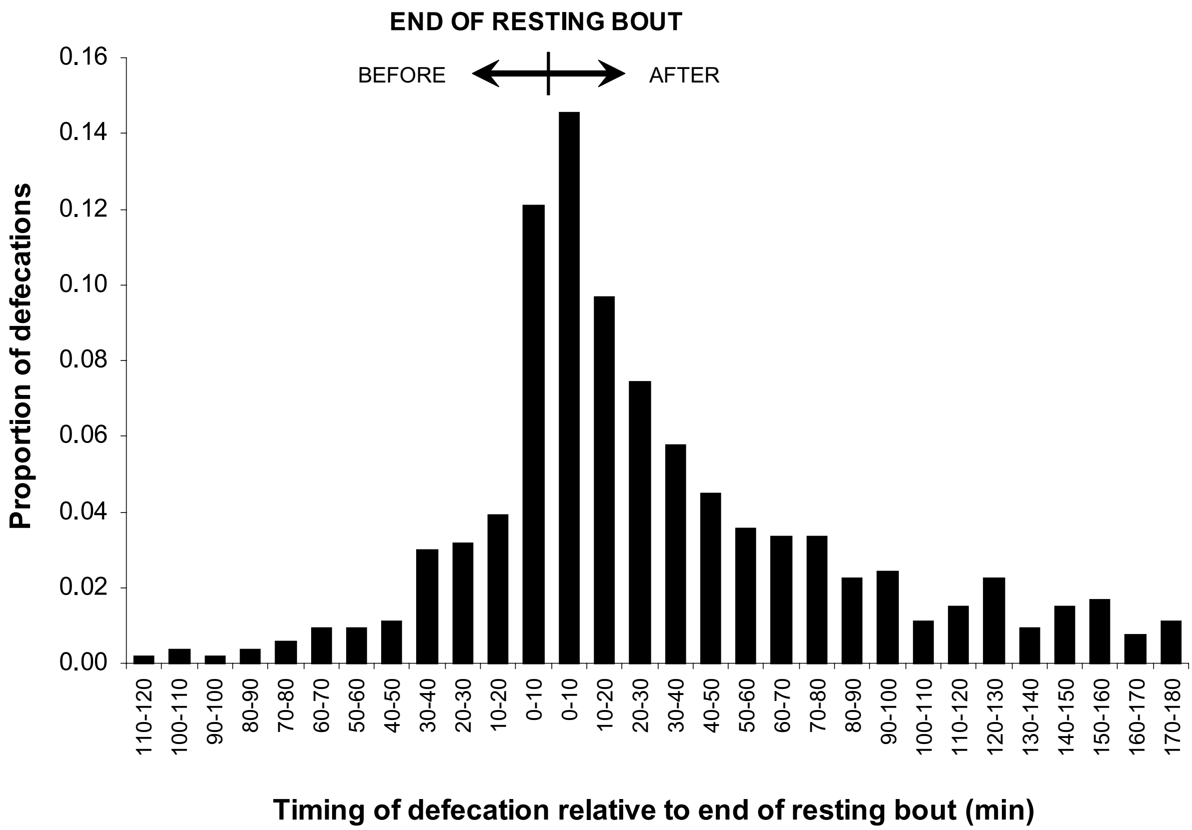

Figure 4. Association between defecation times and resting periods. Of 537 defecations for which we could determine their timing relative to the closest 'long rest' bout (30 min or more), 27% fell within a 10-min window on either side of the end of the bout.

Spider monkeys commonly defecated just before or after the end of resting periods. For example, of a total of 146 defecation events that occurred during bouts of resting or sleeping lasting at least 30 min (mean bout duration for long rests: 1 h 10 min $\pm$ 41 min, N = 85 bouts), 45% occurred within 10 min before the end of the bout, and 20% of 391 defecations occurring after the end of a resting period fell within 10 min of the end the period (Figure 4).

DISCUSSION

Dispersal quantity and seed shadows of spider monkeys

We estimated that one group of spider monkeys dispersed a total of ~13 512 seeds ha^{-1} y^{-1}, with each non-juvenile individual dispersing over 195 500 seeds >1 mm and 39 000 seeds >3 mm during that time. These are clearly minimum estimates of the amount of seeds spider monkeys defecate per ha as (1) we did not collect seeds during the night, and recent studies suggest that the deposition rate under sleeping trees is relatively high (Russo & Augspurger 2004), (2) we were unable to recover all seeds defecated by focal animals (either because they did not fall all the way to the forest floor or because the sample scattered over a broad area), and (3) spider monkey groups have somewhat overlapping home ranges. Additionally, spider monkeys dispersed most of the seeds they swallowed far away from parental trees, thus reducing dispersal limitation – the extent to which the landscape pattern of seed delivery is restricted by processes operating at the dispersal stage (Jordano & Godoy 2002, Schupp *et al.* 2002) – for a wide array of Neotropical species. Our estimate of average dispersal distance (443 m) is comparable to or higher than those reported for a range of other Neotropical primates (e.g. woolly monkeys: Stevenson 2000; howler monkeys: Julliot 1996; capuchins: Wehncke *et al.* 2003, Zhang & Wang 1995), including other populations of *Ateles* (Russo 2003, Zhang & Wang 1995), and our results show that spider monkeys can potentially disperse seeds more than 1250 m away from their sources. Finally, the treatment that swallowed seeds received in the spider monkeys' digestive system did not produce any visible physical damage to those seeds, and, at other sites, gut passage does not seem to aversely affect seed germination rates or alter latency to germination (Stevenson *et al.* 2002). Together, these results suggest that spider monkeys may be key players at the community level in redistributing seeds from many different plant taxa into potential recruitment sites (see Voysey *et al.* 1999a, b, for similar patterns found in western lowland gorillas, *Gorilla gorilla*) and, thus, that their behavioural ecology can potentially have a strong influence on forest community structure and dynamics.

Detailed observations on fruit processing by spider monkeys revealed that adult spider monkeys swallow most of the seeds from the fruits they eat and only rarely spit out or discard seeds underneath or near parental feeding sources. As a result, they potentially incur a very high energetic cost by carrying around non-nutritive loads of indigestible seeds. Link & de Luna (2004), for example, estimated that spider monkeys could ingest up to 1352 g (mean: 289 g, N = 90) of fruits (i.e., more than 15% of their body weight) in a single feeding bout on the palm *Oenocarpus bataua* (Arecaceae), and most of that weight would be made up of indigestible seeds. Furthermore, seeds can occupy significant space in the digestive system that could be filled with other nutritional content. We suggest that the fact that spider monkeys often defecated close to the end of resting periods may reflect a strategy for mitigating the energetic costs of carrying around non-nutritive ballast in the gut. Chapman & Chapman (1991) proposed a similar argument as to why leaf-eating by spider monkeys is concentrated late in the day, before the long nocturnal rest period that can be devoted to digestion. Given the potential costs associated with transporting non-nutritive seeds in the gut, it is intriguing that spider monkeys seldom process fruits in their mouths and spit out the seeds, as many 'cheek-pouching' Old World monkeys do (Lambert 1999).

Several factors influence the seed shadows generated by a seed disperser, including its digestive physiology, diet, body size, movement patterns and social structure (Chapman & Russo, in press). Across their geographic range, spider monkeys have a highly frugivorous diet (Di Fiore & Campbell, in press), their digestive system lacks enlarged chambers that enhance fermentation processes, and they have relatively fast gut passage rates (Milton 1981) that are only slightly shorter than those of woolly monkeys (Stevenson 2000) and much faster than those of other primates of similar body size (Lambert 1998). Fast passage rates can be an adaptation to a diet consisting mainly of ripe fruits, which contain high concentrations of nutrients such as simple carbohydrates and some lipids that are easily extracted in the gut. Additionally, rapid transit times might be interpreted as part of an adaptive strategy to avoid the costs of carrying around large volumes of indigestible material. Either way, by virtue of their short passage times, spider monkeys are able to process high amounts of high-quality fruit per unit time, and, as a consequence, are capable of dispersing a very high number of seeds.

The fission–fusion social structure and ranging behaviour of spider monkeys also influence their pattern of seed dispersal. The average size of a foraging subgroup for spider monkeys is relatively small compared to group size (Chapman *et al.* 1995, Klein & Klein 1977, McFarland 1986), and different subgroups may occupy different areas of the group's home ranges, especially in periods of fruit scarcity (Shimooka 2004). Theoretically, the fact that group members do not all range together could generate a more scattered and uniform distribution of defecated seeds across the landscape compared with that produced by disperser species that ranges in more cohesive groups, which might decrease the likelihood of seed or seedling mortality due to density-dependent factors acting at the site of defecations (Chapman & Russo, in press).

Our data on the locations of defecations indicate precisely such a scattered distribution of seeds, particularly for those defecations that occurred en route between feeding trees and resting bouts, although we also found that some frequently visited areas within the home range (e.g. salt licks) received a relatively heavier fall of seed rain, leading to significant clumping of seeds in a few key areas. Russo (2003) also found that some key sites (e.g. sleeping trees) received a much higher density of seeds than 'in-transit' areas for spider monkeys in Manu National Park, Peru. These results could be taken to imply that the general pattern of defecation by spider monkeys is highly clumped in space, which theoretically would reduce the quality aspects of their dispersal, since seeds deposited in such high-density sites are likely to experience more limited recruitment because of both density-dependent mortality and competition from other plant taxa (Harms *et al.* 2000, Hurtt & Pacala 1995, Russo & Augspurger 2004). Nonetheless, we note that in our study the absolute number of seeds deposited at in-transit sites is actually quite high (Di Fiore & Link, unpubl. data), and, given that these seeds are those least likely to suffer density-dependent mortality, their effects on population structure of tropical tree species is likely to be especially important. Indeed, Russo (2003) found higher seed and seedling survival rates for *Virola calophylla* dispersed to in-transit sites compared to those dispersed under spider monkey's sleeping trees or parental trees. Clearly, more detailed studies of the spatial patterning of defecations across the landscape are needed to evaluate the extent to which vertebrate seed dispersers produce spatially aggregated seed depositions, which can affect seedling establishment and recruitment to later life stages (Cain *et al.* 2000).

The ecological role of ateline primates: implications for forest structure and dynamics

Our results complement those of several other recent studies, which have documented the clear importance of spider monkeys and other ateline primates as dispersers for many species of Neotropical plants (e.g. woolly monkeys: Stevenson 2000; howler monkeys: Andresen 2002, Julliot 1996). First, atelines appear to be particularly important dispersers for plants producing large-seeded fruits or those protected by thick husks (Link & Stevenson 2004; see also Andresen 2000). Most bird species are unable either to open these fruits' husks or to swallow and/or carry their large seeds away from parental feeding patches, and most other arboreal mammalian frugivores (e.g. smaller-bodied primates, kinkajous) and frugivorous bats are also unlikely to be able to swallow and pass large seeds, although secondary dispersal by scatterhoarding rodents can be important for some large-seeded species (Hallwachs 1986, Jansen *et al.* 2002) in addition to altering the initial deposition pattern produced by primary dispersers.

Moreover, even for tree species that bear either small, unprotected fruits or fruits with exposed arils that are potentially dispersed by a wide array of mammals and birds, the proportion of seeds dispersed by ateline primates is nonetheless generally high. In fact, atelines appear to be the primary vertebrate seed dispersers for many species of plant in the Neotropics. For example, in Tinigua National Park, Colombia, three atelines – spider monkeys, woolly monkeys and howler monkeys – together manipulated more than 50% of the entire set of seeds removed from a diverse group of 75 forest tree species (Stevenson 2002). Moreover, in a detailed study of one of these species, *Bursera inversa* (Burseraceae), trees that were accessible to both birds and primates experienced a higher rate of seed removal compared to those trees that were visited by birds alone, highlighting the importance of primate dispersers for this particular taxon (Stevenson *et al.* 2005).

Clearly, spider monkeys and other ateline primates are significant dispersers for many species of plants throughout the Neotropics. These same primates are also among the first animals to go locally extinct in the face of human encroachment into pristine forest areas, even when that encroachment does not involve extensive habitat loss or fragmentation, because primates are often preferred targets for hunters and because they reproduce slowly (Peres 1990). As a consequence of hunting, many Neotropical forests are fast becoming 'empty forests' (Redford 1992), where the vegetation structure remains intact but the forest is largely devoid of large mammals. Because of their importance as dispersal agents, the loss of large-bodied primate frugivores has the potential to dramatically affect the floristic composition and long-term persistence of tropical ecosystems, especially if other disperser species cannot compensate for their lost ecological services (Chapman 1995, Chapman & Chapman 1995, Peres & van Roosmalen 2002). In fact, several recent studies suggest that the loss of primates from tropical ecosystems can have marked effects on recruitment for the plant species comprising the diets of those primates (Chapman & Onderdonk 1998, Cordeiro & Howe 2001, Marsh & Loiselle 2003). It is thus imperative that efforts to conserve and/or manage Neotropical forests pay close attention to the preservation of species such as spider monkeys that act as important seed dispersers for a wide variety of plant species.

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LITERATURE CITED

ALTMANN, J. 1974. Observational study of behaviour: Sampling methods. *Behaviour* 49:227–262.

ANDRESEN, E. 2000. Ecological roles of mammals: the case of seed dispersal. Pp. 2–26 in Entwhistle, A. & Dunstone, N. (eds.). *Priorities for the conservation of mammalian diversity.* Cambridge University Press, Cambridge.

ANDRESEN, E. 2002. Primary seed dispersal by red howler monkey and the effects of defecation patterns on the fate of dispersed seeds. *Biotropica* 34:261–272.

CAIN, M. L., MILLIGAN, B. G. & STRAND, A. E. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87:1217–1227.

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. 1991. The foraging itinerary of spider monkeys: when to eat leaves? *Folia Primatologica* 56:162–166.

CHAPMAN, C. A. & CHAPMAN, L. J. 1995. Survival without dispersers: seedling recruitment under parents. *Conservation Biology* 9:675–678.

CHAPMAN, C. A. & ONDERDONK, D. A. 1998. Forest without primates: primate/plant codependency. *American Journal of Primatology* 45: 127–141.

CHAPMAN, C. A. & RUSSO, S. E. (in press). Primate seed dispersal: linking behavioral ecology and forest community structure. In Bearder, S., Campbell, C. J., Fuentes, A., MacKinnon, K. C. & Panger, M. (eds.). *Primates in perspective.* Oxford University Press, Oxford.

CHAPMAN, C. A., WRANGHAM, R. W. & CHAPMAN, L. J. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36:59–70

CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. Pp. 298–313 in den Boer, P. J. & Gradwell, D. R. (eds.). *Dynamics of populations.* Center for Agricultural Publishing and Documentation, Wageningen.

CORDEIRO, N. J. & HOWE, H. F. 2001. Low recruitment of trees dispersed by animals in Africa forest fragments. *Conservation Biology* 15:1733–1741.

DEFLER, T. R., RODRIGUEZ, J. V. & HERNANDEZ-CAMACHO, J. I. 2003. Conservation priorities for Colombian primates. *Primate Conservation* 19:10–18.

DEW, J. L. 2001. *Synecology and seed dispersal in woolly monkeys* (Lagothrix lagotricha poeppigii) *and spider monkeys* (Ateles belzebuth belzebuth) *in Parque Nacional Yasuní.* Ph.D. Dissertation. University of California at Davis, Davis.

DEW, J. L. & WRIGHT, P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30:425–437.

DI FIORE, A. 1997. *Ecology and behavior of lowland woolly monkeys* (Lagothrix lagotricha poeppigii, *Atelinae*) *in Eastern Ecuador.* Ph.D. Dissertation. University of California at Davis, Davis.

DI FIORE, A. & CAMPBELL, C. J. (in press). The atelines: variation in ecology, behavior, and social organization. In Bearder, S., Campbell, C.J., Fuentes, A., MacKinnon, K.C., & Panger, M. (eds.). *Primates in perspective.* Oxford University Press, Oxford.

DI FIORE, A. & RODMAN, P. S. 2001. Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a Neotropical *terra firma* forest. *International Journal of Primatology* 22:449–480.

EISENBERG, J. F., O'CONNELL, M. A. & AUGUST, P. V. 1979. Density, productivity, and distribution of mammals in two Venezuelan habitats. Pp. 187–209 in Eisenberg, J. F. (ed.). *Vertebrate ecology in the northern Neotropics.* Smithsonian Institution Press, Washington, DC.

FLEMING, T. H., BREITWISCH, R. & WHITESIDES, G. H. 1987. Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics* 18:91–109.

FRANKIE, G. W., BAKER, H. G. & OPLER, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62:881–919.

FRANZEN, M. A. 2005. *Huaorani resource use in the Ecuadorian Amazon: hunting, food sharing and market participation.* Ph.D. Dissertation. University of California at Davis, Davis.

GARBER, P. A. 1986. The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax and Saguinus fuscicollis*). *American Journal of Primatology* 10:155–170.

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

GLANZ, W. E. 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama? Pp. 287–313 in Gentry, A. H. (ed.). *Four Neotropical rainforests.* Yale University Press, New Haven.

HALLWACHS, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril:* Leguminosae). Pp. 285–304 in Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal.* W. Junk Publisher, Dordrecht.

HARMS, K. E., WRIGHT, S. J., CALDERON, O., HERNANDEZ, A. & ALLEN-HERRE, E. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495.

HOWE, H. F. & MIRITI, M. N. 2000. No question: seed dispersal matters. *Trends in Ecology and Evolution* 15:434–436.

HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.

HURTT, G. C. & PACALA, S. W. 1995. The consequences of recruitment limitation: reconciling chance, history, and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.

JANSEN, P. A., BARTHOLOMEUS, M., BONGERS, F., ELZINGA, J. A., DEN OUDEN, J. & VAN WIEREN, S. E. 2002. The role of seed size in dispersal by a scatterhoarding rodent. Pp. 209–225 in Levey, D., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI Publishing, Wallingford.

JANSON, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219:187–189.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104:501–528.

JORDANO, P. & GODOY, J. A. 2002. Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. Pp. 305–321 in Levey, D., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI Publishing, Wallingford.

JORDANO, P. & HERRERA, C. M. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* 2:230–237.

JULLIOT, C. 1996. Seed dispersal by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest of French Guiana. *International Journal of Primatology* 17:239–258.

KLEIN, L. L. & KLEIN, D. B. 1977. Feeding behaviour of the Colombian spider monkey. Pp. 153–181 in Clutton-Brock, T. H. (ed.). *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes.* Academic Press, London.

LAMBERT, J. E. 1997. *Digestive strategies, fruit processing, and seed dispersal in the chimpanzees* (Pan troglodytes) *and redtail monkeys* (Cercopithecus ascanius) *of Kibale National Park, Uganda.* Ph.D. Dissertation. University of Illinois, Urbana-Champaign.

LAMBERT, J. E. 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology* 7:8–20.

LAMBERT, J. E. 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology* 109:365–386.

LAMBERT, J. E. & CHAPMAN, C. A. 2005. The fate of primate-dispersed seeds: Deposition pattern, dispersal distance and implications for conservation. Pp. 137–150 in Forget, P.-M., Lambert, J. E., Hulme, P. E. & Vander Wall, S. B. (eds.). *Seed fate: predation, dispersal and seedling establishment.* CABI Publishing, Wallingford.

LAMBERT, J. E. & GARBER, P. A. 1998. Ecological and evolutionary implications of primate seed dispersal. *American Journal of Primatology* 45:9–28.

LINK, A. & DE LUNA, A. G. 2004. The importance of *Oenocarpus bataua* (Arecaceae) in the diet of spider monkeys at Tinigua National Park, Colombia. *Folia Primatologica* (abstract) 75:391.

LINK, A. & STEVENSON, P. R. 2004. Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia. *Revista Chilena de Historia Natural* 79:319–334.

MARSH, L. K. & LOISELLE, B. A. 2003. Recruitment of black howler fruit trees in fragmented forests of northern Belize. *International Journal of Primatology* 24:65–86.

MCCONKEY, K. R. 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, Central Borneo. *American Journal of Primatology* 52:13–29.

MCFARLAND, M. J. 1986. Ecological determinants of fission-fusion sociality in *Ateles* and *Pan*. Pp. 181–190 in Else, J. G. & Lee, P. C. (eds.). *Primate ecology and conservation.* Cambridge University Press, Cambridge.

MCKEY, D. S. 1975. The ecology of coevolved seed dispersal syndromes. Pp. 159–191 in Gilbert, L. E. & Raven, P. H. (eds.). *Coevolution of animals and plants.* University of Texas Press, Austin.

MILTON, K. 1981. Food choice and digestive strategies of two sympatric primate species. *The American Naturalist* 117:496–505.

PERES, C. A. 1990. Effects of hunting on western Amazonian primate communities. *Biological Conservation* 54:47–59.

PERES, C. A. 1994. Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagothrica cana*) in central Amazonia: comparison with other Atelines. *International Journal of Primatology* 15:333–372.

PERES, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14:240–253.

PERES, C. A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology* 15:1490–1505.

PERES, C. A. & DOLMAN, P. M. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and non-hunted Amazonian forests of varying productivity. *Oecologia* 122:175–189.

PERES, C. A. & VAN ROOSMALEN, M. 2002. Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. Pp. 407–421 in Levey, D., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI Publishing, Wallingford.

POULSEN, J. R., CLARK, C. J. & SMITH, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17:787–808.

REDFORD, K. H. 1992. The empty forest. *BioScience* 42:412–422.

RIDLEY, H. N. 1930. *The dispersal of plants throughout the world.* L. Reeve & Co., Ashford.

ROWELL, T. E. & MITCHELL, B. J. 1991. Comparison of seed dispersal of guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology* 7:269–274.

RUSSO, S. E. 2003. *Linking spatial patterns of seed dispersal and plant recruitment in a neotropical tree,* Virola callophylla (*Myristicaceae*). Ph.D. Dissertation. University of Illinois at Urbana-Champaign.

RUSSO, S. E. & AUGSPURGER, C. K. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla. Ecology Letters* 7:1058–1067.

SCHUPP, E. W. & FUENTES, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2:267–275.

SCHUPP, E. W., MILLERON, T. & RUSSO, S. E. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pp. 19–33 in Levey, D., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI Publishing, Wallingford.

SHIMOOKA, Y. 2004. Seasonal variation in association patterns of wild spider monkeys (*Ateles belzebuth belzebuth*) at La Macarena, Colombia. *Primates* 44:83–90.

SHIMOOKA, Y. 2005. Sexual differences in ranging of *Ateles belzebuth belzebuth* at La Macarena, Colombia. *International Journal of Primatology* 26:385–406.

STEVENSON, P. R. 2000. Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology* 50:275–289.

STEVENSON, P. R. 2002. *Frugivory and seed dispersal by woolly monkeys at Tinigua National Park, Colombia.* Ph.D. Dissertation. State University of New York at Stony Brook.

STEVENSON, P. R., CASTELLANOS, M. C., PIZARRO, J. C. & GARAVITO, M. X. 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., LINK, A. & RAMIREZ, B. H. 2005. Frugivory and seed fate in *Bursera inversa* at Tinigua National Park, Colombia: implications for primate conservation. *Biotropica* 37:431–438.

SUAREZ, S. A. 2003. *Spatio-temporal foraging skills of white-bellied spider monkeys* (Ateles belzebuth belzebuth) *in the Yasuní National Park, Ecuador.* Ph.D. Dissertation. State University of New York at Stony Brook.

TABARELLI, M. & PERES, C. A. 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biological Conservation* 106:165–176.

TERBORGH, J. 1983. *Five New World primates: a study in comparative ecology.* Princeton University Press, Princeton.

TERBORGH, J., PITMAN, N., SILMAN, M., SCHICHTER, H. & NUÑES, V. P. 2002. Pp. 1–17 in Levey, D., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI Publishing, Wallingford.

VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants.* (Third edition). Springer-Verlag, Berlin.

VAN ROOSMALEN, M. G. M. 1985. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazonica* 15:1–238.

VOYSEY, B. C., MCDONALD, K. E., ROGERS, M. E., TUTIN, C. E. G. & PARNELL, R. J. 1999a. Gorillas and seed dispersal in the Lopé Reserve, Gabon. I: Gorilla acquisition by trees. *Journal of Tropical Ecology* 15:23–38.

VOYSEY, B. C., MCDONALD, K. E., ROGERS, M. E., TUTIN, C. E. G. & PARNELL, R. J. 1999b. Gorillas and seed dispersal in the Lopé Reserve, Gabon. II: Survival and growth of seedlings. *Journal of Tropical Ecology* 15:39–60.

WANG, B. C. & SMITH, T. B. 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution* 17:379–385.

WEBB, C. O. & PEART, D. R. 2001. High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. *Ecology Letters* 4:491–499.

WEHNCKE, E. V., HUBBELL, S. P., FOSTER, R. B. & DALLING, J. W. 2003. Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species. *Journal of Ecology* 91:677–685.

WEHNCKE, E. V., NUMA-VALVEZ, C. & DOMINGUEZ, 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.

WRANGHAM, R. W., CHAPMAN, C. A. & CHAPMAN, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10:355–368.

ZHANG, S.-Y. & WANG, L.-X. 1995. Consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica* 27: 397–401.