



# A comparison of inter- and intraspecific variation in seed dispersal in three South American primates

## Research Article

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### Abstract

Primate communities vary in their level of redundancy, or overlap, in seed dispersal function, which could be due to body size, degree of frugivory or intraspecific variation, among other factors. In this study, we quantified redundancy in seed dispersal among three sympatric primate species: *Lagothrix lagothricha*, *Alouatta seniculus* and *Sapajus apella* in gallery forests in Meta, Colombia. We compared the median seed width dispersed and the number and species richness of large ( $\geq 5.9$  mm wide) and very large ( $> 7.5$  mm wide) seeds per faecal sample. The medium-sized, highly folivorous *A. seniculus* mostly dispersed large seeds, the larger, highly frugivorous *L. lagothricha* dispersed very large and small seeds, and the smaller, partially frugivorous *S. apella* dispersed the smallest seeds. However, for *L. lagothricha* and *S. apella*, we did not find the expected results that adults disperse larger seeds than juveniles. Across species, there is complementarity in seed dispersal in relation to seed size, with *L. lagothricha* being unique in its contribution to the dispersal of very large seeds both in terms of quantity and richness.

### Resumen [Español]

Los ensamblajes de primates varían en los papeles como dispersores de semillas, de acuerdo con la redundancia en la sobreposición en la dieta de las especies presentes, tamaño corporal, y grado de frugivoría, entre otros factores. Cuantificamos redundancia entre y dentro de tres primates simpátricos, *Lagothrix lagothricha*, *Alouatta seniculus*, y *Sapajus apella* en su función de dispersión en los bosques de galería de Meta, Colombia. Comparamos el tamaño medio de semillas dispersadas y el número y riqueza de especies de semillas grandes (ancho  $\geq 5.9$  mm) y muy grandes ( $> 7.5$  mm) dispersadas por muestra fecal. *A. seniculus* con tamaño intermedio y altamente folívoro dispersó principalmente semillas grandes; *L. lagothricha*, la especie más grande y altamente frugívora, dispersó principalmente semillas muy grandes y pequeñas; mientras que *S. apella*, el más pequeño y 50% frugívoro, dispersó muchas semillas pequeñas. Para dos especies, *L. lagothricha* y *S. apella*, no encontramos el patrón esperado de que los adultos dispersaron semillas de tamaño más grande de los juveniles. Encontramos complementariedad entre especies en su función de dispersión con relación al tamaño de las semillas, y *L. lagothricha* se caracterizó por su contribución dispersando semillas muy grandes, tanto en términos de cantidad, como en riqueza.

### Introduction

Animal-mediated seed dispersal is critical for the maintenance of plant diversity in tropical ecosystems (Howe 2014). Frugivorous primates play a unique role as seed dispersers, consuming a high diversity of fruits (Poulsen *et al.* 2002, Rosin & Poulsen 2016). They can also manipulate fruits inaccessible to avian dispersers and have lower seed predation rates than many other medium- to large-bodied mammal dispersers (Fuzessy *et al.* 2016, Poulsen *et al.* 2002, Rosin & Poulsen 2016, Zambrano *et al.* 2008). This has resulted in increasing attention in the literature to measuring primate seed dispersal both to better understand how primates shape plant communities and the ecosystem-level implications of primate extinction (Andresen *et al.* 2018). In landscapes that have lost primates, in particular larger primates, plant community composition has changed, resulting in a lesser dominance of large-seeded species with a mammalian dispersal syndrome (Ganzhorn *et al.* 1999, Gardner *et al.* 2019, Koné *et al.* 2008, Stevenson & Aldana 2008, Terborgh *et al.* 2008, Wang *et al.* 2007).

Whether species are redundant or complementary in their seed dispersal function is not known for most primate communities (Chapman & Russo 2007). Redundancy or

**Table 1.** Body mass, per cent of fruit in diet, other food items, and IUCN Red List status of *Lagothrix lagothricha*, *Alouatta seniculus*, and *Sapajus apella*

Species	<i>Lagothrix lagothricha</i>	<i>Alouatta seniculus</i>	<i>Sapajus apella</i>
Body mass (kg)	Males: 7.28–9.27 kg Females: 7.02–7.16 kg <sup>1,2</sup>	Males: 6.31–7.62 kg Females: 4.67–6.02 kg <sup>3,4</sup>	Males: 3.65 kg Females: 2.52 kg <sup>2</sup>
Per cent of fruit in diet	60–80% <sup>5,6</sup>	2–20% <sup>7,8</sup>	50% <sup>9,10</sup>
Other items in diet	Arthropods, flowers, leaves, petioles, roots, stems <sup>5,6</sup>	Leaves, flowers <sup>7,8</sup>	Arthropods, seeds, flowers, shoots, roots, agricultural crops <sup>9,10</sup>
IUCN Red List status	Vulnerable <sup>11</sup>	Least Concern <sup>12</sup>	Least Concern <sup>13</sup>

<sup>1</sup>Peres 1993, <sup>2</sup>Smith and Jungers 1997, <sup>3</sup>Ayres 1986, <sup>4</sup>Rodríguez and Boher 1988, <sup>5</sup>Defler and Defler 1996, <sup>6</sup>Zarate-Caicedo and Stevenson 2014, <sup>7</sup>Julliot and Sabatier 1993, <sup>8</sup>Lopez et al. 2005, <sup>9</sup>Galetti and Pedroni 1994, <sup>10</sup>Izawa 1979, <sup>11</sup>Stevenson et al. 2021b, <sup>12</sup>Link et al. 2021, <sup>13</sup>Boubli et al. 2021

complementarity in a community is specific to an ecological process (such as seed dispersal) or a dimension of that ecological process (such as seed size dispersed, Bueno et al. 2013, Lawton & Brown 1993). Using the example of seed size, redundant communities are ones in which every species disperses the same-sized seeds, while complementary communities are ones in which each species disperses a different range of seed sizes.

The traits of the disperser species, such as body mass and degree of frugivory, affect what plant species it disperses and the quantity and quality of their dispersal (Chen & Moles 2015, Stevenson et al. 2021a). In terms of body mass, all primates disperse small and medium seeds, but only large primates can disperse the largest seeds (Peres & Roosmalen 2002). Additionally, primates that are primarily frugivorous generally disperse a larger quantity of seeds (Sales et al. 2020, Stevenson 2007).

Intraspecific variation in seed dispersal function may result in redundancy across species even if, on average, they appear to be complementary. For instance, juveniles may be less effective in dispersing fruits with hard husks, which require learned skill and strength to process, either avoiding eating these fruits or eating them in smaller quantities than adults (Eadie 2015). Sexual dimorphism in body size or differences in the proportion of fruit in diet between females and males may also result in intraspecific variation in seed dispersal quantity (Koch et al. 2017, Melin et al. 2017). Thus, understanding variation in seed dispersal function requires examining seed dispersal in relation to body size and diet across and within species, the latter pertaining to age/sex class.

We compared inter- and intraspecific variation in the seed dispersal quantity of three sympatric South American primates: the common woolly monkey (*Lagothrix lagothricha*, Atelidae), the Colombian red howler monkey (*Alouatta seniculus*, Atelidae) and the black-capped capuchin (*Sapajus apella*, Cebidae). These species have access to similar plant species, forage socially and are sexually dimorphic, but vary in body mass and degree of frugivory, making them suitable for comparisons. In this study, *L. lagothricha* are the largest in body mass followed by *A. seniculus* and then *S. apella* (Table 1). *L. lagothricha* have the greatest percentage of fruit in their diet, followed by *S. apella*, and then *A. seniculus* (Table 1).

In the Orinoco region of Colombia, where this study takes place, *Lagothrix lagothricha* populations are rapidly declining and are extirpated in some areas (Stevenson et al. 2021b). Areas without *L. lagothricha* differ in plant community composition in relation to the trait of seed size (Stevenson & Aldana 2008), and thus, we will be analyzing differences in seed dispersal among species using this trait. Our study focuses on the quantity of seed

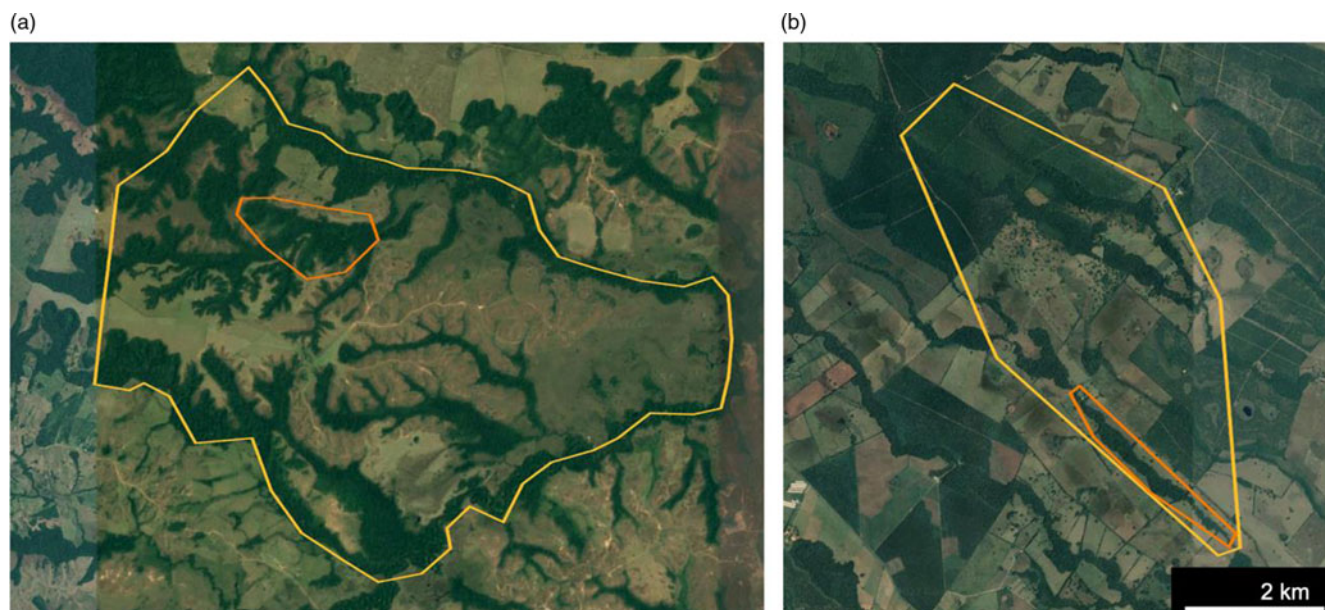
dispersal (i.e., the number of seeds defecated). Not all the seeds found in the faeces will successfully recruit (seed dispersal quality). However, *L. lagothricha* and *A. seniculus* are primarily seed dispersers, rather than seed predators (Benítez-Malvido et al. 2014, Stevenson 2000). *Lagothrix* spp. are seed predators for 6% of the species they eat and occasionally seed predators for 16% (Stevenson et al. 2002). *Alouatta* spp. are seed predators for only 1% of the species they eat and occasionally predate 6% (Stevenson et al. 2002). Thus, the presence of intact seeds in their faeces almost always indicates that they can disperse those species. *S. apella* can be seed dispersers or predators, but the predated seeds are usually masticated or spit out, making them distinct from those with the potential to successfully recruit (Bossier et al. 2020, Galetti & Pedroni 1994, Julliot et al. 2001).

We first ask how the overall seed dispersal function of primates varies among and within species predicting: (1) among species, the largest species, *Lagothrix lagothricha*, will disperse the largest median seed size, followed by *Alouatta seniculus*, and then *Sapajus apella*. Within species, the largest individuals, adult males, will disperse the largest seed size, followed by adult females and then juveniles. (2) Even in cases where species are complementary, some of their age/sex classes will be redundant (i.e., there will be redundancy among species, but only when considering age/sex class). We also ask how the dispersal of large seeds ( $\geq 5.9$  mm, including very large seeds) and very large seeds ( $> 7.5$  mm) differs among and within species, predicting the following: (1) among species, the largest species, *L. lagothricha*, will disperse the greatest number of large and very large seeds per faecal sample, followed by *A. seniculus*, and then *S. apella*, which we predict cannot disperse very large seeds. Within species, the largest individuals, adult males, will disperse the greatest number of large and very large seeds, followed by females, and then juveniles. (2) Due to their higher degree of frugivory, *L. lagothricha* will disperse the greatest number of plant species, including the large- and very large-seeded plant species on which we focus in this study. *A. seniculus* will disperse more very large-seeded plant species than *S. apella*, which will not disperse very large seeds due to their small body size. However, *S. apella* will disperse more large-seeded species than *A. seniculus* because both species can disperse these seeds; however, *S. apella* is more frugivorous.

## Materials and methods

### Study sites

Two of the authors, KNE and JRO, conducted fieldwork in Santa Rosa and Rey Zamuro in Meta, Colombia, which are located ~23 km



**Figure 1.** Satellite images of a. Rey Zamuro and b. Santa Rosa outlined in yellow. The forest outlined in orange within the sites is where the study groups live. The study sites are ~23 km apart. Images are from Google Earth (Google 2022).

apart. Rey Zamuro (73°23'W, 03°32'N) is a 300-ha reserve established in 1998 (Sandino 2006). It is 260 msl and has an average temperature of 25.6°C and annual precipitation of 2513 mm (IDEAM 2019). This reserve consists of gallery forests and some fragments, pasture and savanna. Santa Rosa (73°38'W, 03°36'N) is 350 msl and has a mean temperature of 28°C and annual precipitation of 2000–2500 mm (Obregón 2007). It is a cattle ranch with a total area of around 365 ha, including 50 ha of gallery forest in three fragments (Caro & Ardila 2004). At both sites, the primate groups observed occupied only a subset of the area of the full site (for *Lagothrix lagothricha*, an area of forest around 150 ha and for *Alouatta seniculus* and *Sapajus apella*, a 32-ha fragment, Figure 1). In both cases, this area is surrounded by pasture and the forest is occasionally used by cattle (Caro & Ardila 2004, pers. obs.). Both sites have intermediate values of tree diversity (between 64 and 119 species/hectare), and the vegetation is dominated by species in the Burseraceae, Moraceae, Clusiaceae, Peraceae and Fabaceae families (Stevenson & Aldana 2008). Based on data from 1-ha vegetation plots at each site, the sites have a Jaccard Index, number of shared genera (31) over number of total genera (107, 84 in Rey Zamuro and 54 in Santa Rosa), of 29, indicating they are dissimilar (Janson & Vegelius 1981). However, the widths of seeds dispersed by endozoochory in these plots do not differ (Appendix S1, Supplementary dataset 3). Most of the data collection for all species happened during the rainy season (March–November) when most species fruit (Chacón-Moreno 2004, Monasterio & Sarmiento 1976).

### Data collection

We used two datasets in this study, one on *Lagothrix lagothricha* at Rey Zamuro (Supplementary dataset 1) and one on *Alouatta seniculus* and *Sapajus apella* at Santa Rosa (Obregón 2007, Supplementary dataset 2). These species were sympatric in the study region prior to the extirpation of *L. lagothricha*. At Rey Zamuro, we followed a group of reintroduced *Lagothrix lagothricha*, including two adult females, one adult male and one juvenile/sub-adult female. We define juveniles in this study as

individuals that have been weaned but have not yet bred. For one of the adult females, we collected faecal samples from November 2018 to March 2020; however, the other adult female was predated in March 2019 and thus faecal sample collection from her stopped after that. The adult male and juvenile were released in November 2019, which is when our data collection on these individuals commenced. All individuals underwent *in situ* rehabilitation and had their diet supplemented for the first 5 months post-release. Most of the faecal samples came from January to August, throughout which *L. lagothricha* consumed seeds representative of the smallest and largest seeds they dispersed in this study. The exception was in June and July when they only consumed a few species with seeds larger than 5.48 mm. We washed all faecal samples using a sieve with 0.5 mm mesh (smallest seeds found were 1 mm wide). Then, we counted and identified all intact seeds to the species level and measured the length and width (the second largest axis of the seed) of 5–10 seeds from most species. Usually, we were able to assign species status for seeds, but in a few cases, we could only determine the genus and treated them as morphospecies (e.g., *Protium* sp. 1). From this dataset, we used all faecal samples for which the seeds were identified, resulting in 187 samples for *L. lagothricha* (35 from adult males, 119 from adult females and 33 from juveniles).

At Santa Rosa, we followed one group of *Alouatta seniculus* (two adult males, two adult females, two juveniles) and one group of *Sapajus apella* (one adult male, one adult female and one juvenile) for four months (September to December 2006). For both species, we conducted focal follows for five days every month, with adult males followed for two of the days, adult females for two of the days and juveniles for one day, collecting all faecal samples from these individuals during the follows. We collected most *A. seniculus* faecal samples in the middle of the day when the group members defecate together, as it was easiest to identify which faecal samples came from which individuals at that time. Similar to *L. lagothricha*, throughout the period of collection, *A. seniculus* and *S. apella* consumed seeds representative of the smallest and largest seeds they dispersed in this study.

We counted and identified all intact seeds greater than 1 mm in length (smallest seed was 0.8 mm wide) to the species level and measured the length and width of 30 seeds of each species. For seeds that were 1–3 mm long, we divided the sample into quadrats, counted the seeds in one quadrat and multiplied this by 4 to estimate the total number of seeds in the faecal sample. We identified all seeds to the species level or, if not possible, to the genus level and used morphospecies. Our dataset resulted in 57 samples for *A. seniculus* (24 from adult males, 24 from adult females, 9 from juveniles) and 110 samples for *S. apella* (50 from adult males, 36 from adult females, 24 from juveniles).

### Statistical analysis

We quantified seed dispersal in three ways: (1) the overall median seed size dispersed for each species and age/sex class within that species (adult male, adult female, juvenile); (2) the mean number of large and very large seeds per faecal sample, as measured using the Poisson parameter  $\lambda$  for each species and age/sex class within that species; and (3) the richness of large and very large seeds dispersed, as estimated using Bernoulli product sample-based extrapolation (Supplementary code 1). All these metrics are based on seed width. We chose to use width rather than length as it is the limiting dimension in the ability of the primate to swallow the seed whole, and thus, frugivore selection acts on seed width rather than length, which can vary more (Mazer & Wheelwright 1993). We performed all analyses in RStudio v1.3.1093 (RStudio Team 2020).

Using a permutation test, we determined the widths of seeds dispersed at the species level had unequal variances for some of the pairs of species (Appendix S2). Therefore, we use the Fligner-Policello test to compare median seed width dispersed by different species and age/sex classes using the R package RVAideMemoire (Hervé 2021). The Fligner-Policello test is similar to the rank-based two-sample Wilcoxon-Mann-Whitney test, although it does not assume equal variances. It accounts for the variance of each of the groups in the test statistic,  $U$  (Fligner & Policello 1981). In this analysis, we did not include *Dipteryx micrantha* (width = 20 mm), which we only found in the faeces of *L. lagothericha*, in the analysis as there were not seeds of comparable size known to be available to *A. seniculus* and *S. apella* during the data collection period. For analyses excluding the smallest seeds, which *L. lagothericha* and *S. apella* consumed in the hundreds to thousands, see Appendix S3. We applied a Bonferroni correction, using a significance level of  $\alpha = 0.05/16 = 0.003$ , to address the potential of inflated Type I error due to multiple comparisons (Dunn 1961).

Second, we compared the number of large and very large seeds per faecal sample for each species and age/sex class within species. We defined very large seeds as those with a width greater than 7.5 mm and large seeds as those with a width greater than or equal to 5.9 mm. In the analyses, the large seed category encompasses the very large seed category. The threshold of 1 cm in length is often used to define large seeds; however, there is not a commonly used equivalent in width (Markl et al. 2012, Stevenson et al. 2005). Therefore, we chose our thresholds such that 25% of the species dispersed were considered 'very large' and 50% were considered 'large'. Not all the age/sex classes of *Alouatta seniculus* and *Sapajus apella* dispersed very large seeds, and thus, we only do the intraspecific comparisons of age/sex classes for very large seeds for *Lagothrix lagothericha*.

As this is count data, we assumed a Poisson distribution and found the value of  $\lambda$  for each species and age/sex class for which the negative log-likelihood (NLL) was at its minimum (Bolker 2007).

The NLL of the Poisson distribution is:

$$NLL = \sum_{i=1}^n (\lambda - x_i \log(\lambda) + \log(x_i!)) \quad (1)$$

where  $x_i$  is the number of large or very large seeds/faecal sample for species or age/sex class  $i$ . For very large seeds, we found the NLL for all values from 0, the minimum number of seeds/faecal sample, to 14, the maximum, at intervals of 0.01, while for large seeds, we searched for the NLL in the range of 0 to 94, as above this yielded NLL values of negative infinity. Then, we compared  $\lambda$  values using 99.8 per cent confidence intervals. We used the threshold for significance of  $\alpha = 0.05/18 = 0.002$  as we did 18 comparisons (Dunn 1961).

For both the overall median seed size dispersed and the  $\lambda$  of the number of large and very large seeds/faecal sample, we made two sets of comparisons: (1) among species and (2) among age/sex classes within species (adult males, adult females and juveniles). For the overall median seed size dispersed, we also did post hoc comparisons between age/sex classes that differed from other classes within its species and the other species.

Finally, we determined the contribution of each species to large- and very large-seeded dispersal in terms of the number of plant species they dispersed. We only did this analysis at the primate species level as not all age/sex classes within *Alouatta seniculus* and *Sapajus apella* dispersed very large seeds. We used Bernoulli product sample-based extrapolation to estimate the number of large and very large-seeded species we would have found each primate species to disperse had we collected as many samples for *A. seniculus* and *S. apella* as we did for *L. lagothericha*. This is calculated as follows (Colwell et al. 2012):

$$s_{i,187} = s_{obs} + \hat{Q}_0 \left[ 1 - \left( 1 - \frac{Q_1}{Q_1 + T\hat{Q}_0} \right)^{t^*} \right] \quad (2)$$

where  $s_{i,187}$  is the estimated number of species with large or very large seeds dispersed by species  $i$  if we had collected 187 faecal samples,  $s_{obs}$  is the observed number of large or very large-seeded species dispersed by that species,  $Q_1$  is the number of species found in only one faecal sample,  $T$  is the number of faecal samples collected, and  $t^*$  is the number of faecal samples needed to reach a sample size of 187. The uncertainty in this equation comes from  $\hat{Q}_0$ , which is the estimated number of large or very large-seeded plants that the primate disperses, but we did not find in our samples (Chao 1987). We estimated the value for  $\hat{Q}_0$  and its 95<sup>th</sup> per cent confidence intervals in the R package Spade (Species Prediction and Diversity Estimation, Chao et al. 2016).

### Ethical statement

The authors assert that all procedures contributing to this work comply with the Regional Governmental Institution (Cormacarena) permit 1376 of June 27, 2013 'to collect specimens of wild species of biological diversity for non-commercial scientific research'. This study also complies with the Universidad de Los Andes ethics committee guidelines on the care and use of regulated animals.

### Results

We collected a total of 354 faecal samples, which contained 53454 seeds of 43 plant species (Table 2). *Lagothrix lagothericha* dispersed

**Table 2.** The sample size and species richness of all seeds and large- and very large-seeded species, and the range of seed widths of the dispersed seeds for *Lagothrix lagothricha*, *Alouatta seniculus*, and *Sapajus apella*. The faecal samples for *L. lagothricha* are from Rey Zamuro (November 2018 to March 2020) and for *A. seniculus* and *S. apella* are from Santa Rosa (September to December 2006), both located in Meta, Colombia

Species	<i>Lagothrix lagothricha</i>	<i>Alouatta seniculus</i>	<i>Sapajus apella</i>
Number of faecal samples	187	57	110
Total number of plant species	22	9	18
Total number of seeds	4032	3960	45462
Number of large-seeded species (per cent of large-seeded species in faecal samples)	14 (16%)	6 (57%)	7 (1%)
Number of very large-seeded species (per cent of large-seeded species in faecal samples)	7 (6%)	2 (0.3%)	3 (0.01%)
Range of seed widths dispersed (mm)	1.0–20	4.6–9.8	0.8–9.8

**Table 3.** Comparisons in the median seed width dispersed by *Lagothrix lagothricha* (Ll), *Alouatta seniculus* (As), and *Sapajus apella* (Sa) across species, within species among adult males (M), adult females (F), and juveniles (J), and post hoc comparisons. Represented is the U statistic and p-value. In bold are significant results ( $p < 0.003$ ). For the results of the analysis excluding seeds  $< 1.1$  mm, refer to Appendix S3. Sample sizes, equal to the number of seeds dispersed, are as follows: *L. lagothricha* (total: 4017, adult males: 360, adult females: 3455, juveniles: 202), *A. seniculus* (total: 3960, adult males: 1595, adult females: 1898, juveniles: 467), *S. apella* (total: 45462, adult males: 20511, adult females: 24469, juveniles: 482)

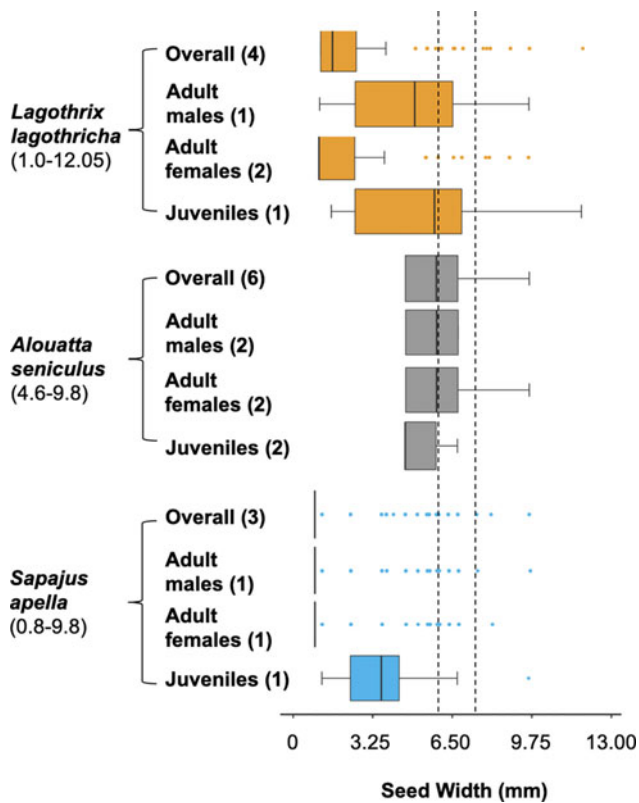
Hypothesis	Comparisons	U Statistic	p-value	Result
Interspecific comparison				
Ll > As > Sa	<b>Ll (1.50) vs. As (5.90)</b>	<b>71.7</b>	<b>&lt;0.001</b>	As > Ll > Sa
	<b>Ll (1.50) vs. Sa (0.80)</b>	<b>-529.8</b>	<b>&lt;0.001</b>	
	<b>As (5.90) vs. Sa (0.80)</b>	<b>-1474.4</b>	<b>&lt;0.001</b>	
Intraspecific comparison				
Ll: M > F > J	<b>M (5.00) vs. F (1.00)</b>	<b>-30.5</b>	<b>&lt;0.001</b>	J > M > F
	<b>J (5.85) vs. M (5.00)</b>	<b>-3.2</b>	<b>0.001</b>	
	<b>J (5.85) vs. F (1.00)</b>	<b>-26.7</b>	<b>&lt;0.001</b>	
As: M > F > J	M (5.90) vs. F (5.90)	1.3	0.197	M = F > J
	<b>J (4.60) vs. M (5.90)</b>	<b>6.4</b>	<b>&lt;0.001</b>	
	<b>J (4.60) vs. F (5.90)</b>	<b>7.2</b>	<b>&lt;0.001</b>	
Sa: M > F > J	<b>M (0.80) vs. F (0.80)</b>	<b>3.9</b>	<b>0.001</b>	J > F > M
	<b>J (3.60) vs. M (0.80)</b>	<b>-486.2</b>	<b>&lt;0.001</b>	
	<b>J (3.60) vs. F (0.80)</b>	<b>-474.9</b>	<b>&lt;0.001</b>	
Post hoc comparison				
LlJ and As	LlJ (5.85) vs. As (5.90)	0	0.986	LlJ = As
LlF and Sa	<b>LlF (1.00) vs. Sa (0.80)</b>	<b>-492.4</b>	<b>&lt;0.001</b>	LlF > Sa
AsJ and Ll	<b>AsJ (4.60) vs. Ll (1.50)</b>	<b>-59.8</b>	<b>&lt;0.001</b>	AsJ > Ll
SaJ and Ll	<b>SaJ (3.60) vs. Ll (1.50)</b>	<b>-22</b>	<b>&lt;0.001</b>	SaJ > Ll

22 species, *Alouatta seniculus* dispersed 9, and *Sapajus apella* dispersed 18 (Table 2). The three primate species dispersed 18 species with large seeds and 10 species with very large seeds. Overall, 6% of the seeds in the faecal samples were large (width  $\geq 5.9$  mm), and 0.5% were very large (width  $> 7.5$  mm).

Overall, *Lagothrix lagothricha* dispersed seeds that were 1.0–12.05 mm wide (and the excluded species, *Dipteryx micrantha*, which is 20 mm), *Alouatta seniculus* dispersed seeds 4.6–9.8 mm wide, and *Sapajus apella* dispersed seeds 0.8–9.8 mm wide (see Supplementary datasets 1 and 2 for the individual plant species dispersed by each primate). When examining all seeds dispersed, we found, as predicted, that *L. lagothricha* (FP Test:  $U = -529.8$ ,  $p < 0.001$ ) and *A. seniculus* (FP Test:  $U = -1474.4$ ,  $p < 0.001$ )

dispersed a larger median seed width than *S. apella* (Table 3, Figure 2). Contrary to predictions, *A. seniculus* dispersed a larger median seed width than the largest primate, *L. lagothricha* (FP Test:  $U = -71.7$ ,  $p < 0.001$ , Table 3, Figure 2).

When comparing overall seed dispersal within species, we found that contrary to predictions, *Lagothrix lagothricha* juveniles dispersed a larger median seed width than adult males (FP Test:  $U = -3.2$ ,  $p = 0.001$ ), which dispersed a larger median seed width than adult females (FP Test:  $U = -30.5$ ,  $p < 0.001$ , Table 3, Figure 2). *Alouatta seniculus* adult males and females dispersed the same median seed width (FP Test:  $U = 1.3$ ,  $p = 0.197$ ), while juveniles dispersed a smaller seed width than adult males (FP Test:  $U = 6.4$ ,  $p < 0.001$ ) and adult females (FP Test:  $U = 7.2$ ,  $p < 0.001$ ),



**Figure 2.** Boxplots of the widths (mm) of seeds dispersed by each species (*Lagothrix lagothricha*: N = 4032 seeds, *Alouatta seniculus*: N = 3960, *Sapajus apella*: N = 45462) and age/sex class (adult males, adult females, juveniles). These boxplots do not include *Dipteryx micrantha* (20 mm), as this species was excluded from this analysis. The faecal samples for *L. lagothricha* are from Rey Zamuro (November 2018 to March 2020) and for *A. seniculus* and *S. apella* are from Santa Rosa (September to December 2006), both located in Meta, Colombia. Line: median, box: interquartile range, points: outliers, defined as greater than 1.5 times the interquartile range away from the first or third quartile. Note that due to the large number of small seeds in the faeces of adult *S. apella*, the interquartile range is much smaller than for other species and age/sex classes and thus appears as a line in the figure. Under each species name is the range of seed sizes (included in the statistical analyses) it dispersed and next to each age/sex class is the number of individuals sampled. The dotted lines represent the thresholds for 'large' and 'very large' seeds used in this study:  $\geq 5.9$ ,  $> 7.5$ ). For the results of the analysis excluding seeds  $< 1.1$  mm, refer to Appendix S3.

Table 3, Figure 2). *Sapajus apella* adult males dispersed a smaller median seed width than females (FP Test:  $U = 3.9$ ,  $p = 0.001$ ) and the smallest individuals, juveniles, dispersed a larger median seed width than adult males (FP Test:  $U = -486.2$ ,  $p < 0.001$ ) and adult females (FP Test:  $U = -474.9$ ,  $p < 0.001$ , Table 3, Figure 2).

*Lagothrix lagothricha* adult females (FP Test:  $U = -492.4$ ,  $p < 0.001$ ) and *Alouatta seniculus* juveniles (FP Test:  $U = -59.8$ ,  $p < 0.001$ ), although statistically different from the rest of the individuals in their species in terms of the median seed width they dispersed, were not redundant (i.e., did not overlap) with other species (Table 3, Figure 2). *L. lagothricha* and *Sapajus apella* juveniles, however, were redundant with other species, with *L. lagothricha* juveniles dispersing the same median seed width as *A. seniculus* (FP Test:  $U = 0.0$ ,  $p = 0.986$ , Table 3, Figure 2) and *S. apella* juveniles dispersing a larger median seed width than *L. lagothricha* (FP Test:  $U = -22.0$ ,  $p < 0.001$ , Table 3, Figure 2).

*Alouatta seniculus* dispersed the greatest number of large seeds ( $\geq 5.9$  mm) per faecal sample (99.8 per cent confidence interval: 37.25, 42.40), followed by *Sapajus apella* (CI: 4.21, 5.49) and then *Lagothrix lagothricha* (CI: 3.03, 3.86, Table 4). All age/sex classes of

*L. lagothricha* dispersed similar numbers of large seeds per faecal sample (CI: adult males: 3.04, 5.15, adult females: 2.89, 3.92, juveniles: 2.19, 4.06, Table 4). *A. seniculus* adult males (CI: 35.99, 43.94) and females (CI: 42.53, 51.15) dispersed similar numbers of large seeds per faecal sample, while juveniles dispersed fewer (CI: 16.73, 26.20). In *S. apella*, adult females (CI: 5.15, 7.74) dispersed more large seeds than males (CI: 3.16, 4.89), while juveniles did not differ from either of the adult sex classes (CI: 3.12, 5.73, Table 4). *L. lagothricha* dispersed the most large-seeded species (14 species), followed by *A. seniculus* (95<sup>th</sup> per cent confidence interval; 7.90, 8.19) and then *S. apella* (CI: 7.67, 7.68 species).

For the dispersal of very large-seeded plants ( $> 7.5$  mm wide), as predicted, *Lagothrix lagothricha* dispersed the greatest number of very large seeds per faecal sample (99.8 per cent confidence interval: 1.10, 1.62 seeds per faecal sample). *Alouatta seniculus* (CI: 0.05, 0.38 seeds per faecal sample) and *Sapajus apella* (CI: 0.02, 0.16 seeds per faecal sample) dispersed similar numbers of very large seeds per faecal sample (Table 4). Only *A. seniculus* adult females and *S. apella* adults dispersed very large seeds. *L. lagothricha* adult males (CI: 1.27, 2.74 seeds per faecal sample), adult females (CI: 0.89, 1.48 seeds per faecal sample) and juveniles (CI: 0.88, 2.16 seeds per faecal sample) dispersed similar numbers of very large seeds per faecal sample (Table 4). Finally, in terms of the richness of very large seeds dispersed, as expected, *L. lagothricha* dispersed more very large-seeded species (7 species) than *A. seniculus* (95<sup>th</sup> per cent confidence interval: 3.36, 3.69 species) and *S. apella* (CI: 3.62, 3.67 species).

## Discussion

Our analysis demonstrated that *Lagothrix lagothricha*, *Alouatta seniculus* and *Sapajus apella* are complementary in their seed dispersal function in terms of seed size, as is in line with our predictions. Our observations across species align with prior studies showing species that are primarily frugivores disperse a greater richness of plant species and larger seeds are more likely to be consumed by larger primates (Fuzessy et al. 2018). However, when comparing within species, we found that, despite being smaller, juveniles dispersed a similar median seed size to adults and, in the case of *L. lagothricha* and *S. apella*, similar numbers of large seeds per faecal sample.

Although *Lagothrix lagothricha* dispersed a smaller median seed width than *Alouatta seniculus*, they were critical in the dispersal of very large seeds. *L. lagothricha* was the only species in which adult males, adult females and juveniles all dispersed very large seeds, and they dispersed the greatest number of large- and very large-seeded plant species. The adult females also dispersed the largest seed found in this study, *Dipteryx micrantha*, which is 20 mm in width. This supports observations at other sites of *L. lagothricha* dispersing high quantities and richness of large-seeded plants (Fuzessy et al. 2018, Stevenson 2000, Stevenson et al. 2005). *L. lagothricha* also contributed to the dispersal of some of the smallest seeds in this study, with adult females and males dispersing hundreds of *Ficus* sp. seeds (1 mm in width). Excluding these from the analysis would have resulted in *L. lagothricha* dispersing a larger median seed size than *A. seniculus* (Appendix S3). Additionally, *L. lagothricha* have a high seed dispersal quality, with digestion that decreases latency to germination and has a neutral or positive effect on germination rates (in 15 of 16 species studied, Stevenson et al. 2002), and with an average dispersal distance of 150–500 m (Stevenson 2000). Compared to other plant species, *Ficus* sp. seeds appeared in large numbers per faecal

**Table 4.** Comparisons of the number of large ( $\geq 5.9$  mm wide) and very large ( $> 7.5$  mm) seeds dispersed per faecal sample among *Lagothrix lagothericha* (Ll), *Alouatta seniculus* (As), and *Sapajus apella* (Sa) and adult male (M), adult female (F), and juvenile (J) age/sex classes. Represented is the mean and 99.8 per cent confidence intervals of the maximum likelihood estimate of the Poisson parameter  $\lambda$ . Sample sizes, equal to the number of faecal samples collected, are as follows: *L. lagothericha* (total: 187, adult males: 35, adult females: 119, juveniles: 33), *A. seniculus* (total: 57, adult males: 24, adult females: 24, juveniles: 9), *S. apella* (total: 110, adult males: 50, adult females: 36, juveniles: 24)

Hypothesis	Lambda (large)	Lambda (very large)	Results
Interspecific comparison			
<i>Lambda</i> : Ll > As > Sa	Ll: 3.43 (3.03, 3.86)	Ll: 1.34 (1.10, 1.62)	Large: As > Sa > Ll
	As: 39.77(37.25, 42.40)	As: 0.16 (0.05, 0.38)	Very large:
	Sa: 4.82 (4.21, 5.49)	Sa: 0.06 (0.02, 0.16)	Ll > As = Sa
Intraspecific comparison			
<i>Lambda</i> : LIM > LIF > LIJ	LIM: 4.00 (3.04, 5.15)	LIM: 1.91 (1.27, 2.74)	LIM = LIF = LIJ
	LIF: 3.38 (2.89, 3.92)	LIF: 1.16 (0.89, 1.48)	
	LIJ: 3.03 (2.19, 4.06)	LIJ: 1.42 (0.88, 2.16)	
<i>Lambda</i> : AsM > AsF > AsJ	AsM:39.83(35.99, 43.94)		AsM = AsF > AsJ
	AsF:46.71(42.53, 51.15)		
	AsJ:21.11(16.73, 26.20)		
<i>Lambda</i> : SaM > SaF > SaJ	SaM: 3.96 (3.16, 4.89)		SaF > SaM
	SaF: 6.36 (5.15, 7.74)		SaF = SaJ
	SaJ: 4.29 (3.12, 5.73)		SaM = SaJ

sample. Therefore, we would expect germination rates to be low for this species; however, secondary dispersal can improve germination (Andresen 1999).

*Alouatta seniculus*, the second largest and least frugivorous primate in this study, dispersed several species with large seeds, but contributed little to the dispersal of species with small or very large seeds. Contrary to previous findings, *A. seniculus* dispersed a greater richness of large-seeded plants than *Sapajus apella* despite being primarily folivorous (Bufalo *et al.* 2016, Julliot & Sabatier 1993, Lopez *et al.* 2005). This may be because *A. seniculus* mostly consumed large-seeded species in this study, although they have been observed dispersing *Ficus* and other small seeds (Stevenson *et al.* 2000). *A. seniculus* provided most of the dispersal for these species, as *Lagothrix lagothericha* mostly dispersed smaller and very large seeds and *Sapajus apella* mostly dispersed smaller seeds. Similar to *L. lagothericha*, *Alouatta* species provide high-quality dispersal. Their digestion decreases the latency to germination and has a neutral to positive effect on germination of seeds (in all 5 species studied, Benítez-Malvido *et al.* 2014, in 6 of 7 species studied, Stevenson *et al.* 2002). Additionally, they disperse seeds at an average distance of 290 m (Julliot *et al.* 2001). Their mass defecation patterns attract dung beetles, which perform secondary dispersal (Fuzessy *et al.* 2021).

*Sapajus apella* dispersed mostly smaller seeds, including the smallest seed in this study, *Miconia ternatifolia* (0.8 mm in width). Although *Lagothrix lagothericha* and *Alouatta seniculus* dispersed smaller seeds, *S. apella* dispersed the smallest seeds on average, which we expected given their smaller body size. Only the adults dispersed very large seeds, at the upper range of what has been recorded to be dispersed by *S. apella* (Julliot *et al.* 2001). In terms of their overall seed dispersal, *S. apella* were redundant with *L. lagothericha* in their dispersal of mostly smaller seeds, but not very large seeds. They had almost no redundancy in terms of seed

size with *A. seniculus*. There has been little research on seed dispersal quality for *S. apella*, but past findings suggest they have an average dispersal distance of 390 m and that their gut passage does not affect germination rates or latency (Julliot *et al.* 2001). Similar to *Ficus* sp. in the faeces of *L. lagothericha*, seeds of *M. ternatifolia* are unlikely to have high germination rates without secondary dispersal (Andresen 1999).

There was less intraspecific variation than expected and what we did find contrasted with predictions based on body size, except for *Alouatta seniculus* juveniles dispersing a smaller median seed width than the adults. *A. seniculus* juveniles and *Lagothrix lagothericha* adult females did not differ enough from the other individuals in their species as to be redundant with other species. However, *L. lagothericha* juveniles dispersed the same median seed width as *A. seniculus*, and *Sapajus apella* juveniles dispersed a greater median seed width than *L. lagothericha*. There are factors that affect what fruits certain age/sex classes consume that are unrelated to seed size but may contribute to the differences in dispersal seen in *L. lagothericha* and *S. apella* juveniles. It has been argued that some fruits require learned skill or strength to process, which may result in juveniles dispersing fewer seeds of certain species in general (Eadie 2015). However, for our study species it is common for all age-sex classes to feed from the food items preferred by each species (Stevenson *et al.* 2000).

For *Sapajus apella*, this may be in part due to differential habitat use, as *S. apella* juveniles can forage on smaller branches due to their small size and spend more time playing on the ground. This can result in them consuming fruits of small, understory plants at greater frequencies than adults (Wheeler & Hammerschmidt 2013, Williamson *et al.* 2021). For example, juveniles dispersed nearly half of the seeds of *Psychotria* spp. in this study, which come from small, understory trees. Juvenile *L. lagothericha* tend to eat less fruit than adults and are subject to displacement from fruiting trees by

adult males, which could lead to differences in the proportions of preferred species of fruit in juvenile vs. adult male diets (Gonzalez et al. 2016, Stevenson et al. 1994). However, for *L. lagothericha*, these results contrast with what was found at the nearby Tinigua National Park, where juveniles (N = 5-8) preferred smaller-sized seeds (Stevenson et al. 2005). Our results may be due to the available fruits during the limited study period and preferences of the individual juvenile in this study. Finally, for both species, we observed different age/sex classes on different days, so differences in frequency may also have resulted from changing availability of fruits over the observation period.

Further research is needed to understand whether these patterns in seed dispersal by *Lagothrix lagothericha*, *Alouatta seniculus*, and *Sapajus apella* at Santa Rosa and Rey Zamuro are seen more broadly in these species. Our sample sizes were limited as the small fragments of these sites could only support small social groups. Additionally, *L. lagothericha* at this site were reintroduced, which may affect their foraging behaviour (Ramírez & Stevenson 2020).

Our finding of the unique role of *Lagothrix lagothericha* in dispersing very large-seeded plants is consistent with observations in this region. Fragments without *L. lagothericha* have been found to have different plant assemblages, dominated by smaller-seeded plants, than those with this disperser (Stevenson & Aldana 2008). Although *Alouatta seniculus* and *Sapajus apella* are still present in many forests fragmented by agriculture due to their higher tolerance of human disturbance (Benchimol & Peres 2014, Crockett 1998, Michalski & Peres 2005), they are not performing the same seed dispersal function as *L. lagothericha*. This study focused on how this could result in a loss of dispersal for large-seeded species, but there are likely other plant traits with changing frequencies in these communities due to the loss of *L. lagothericha*. *L. lagothericha* contributes to the dispersal of a large richness of species and their loss is unlikely to be fully compensated by *A. seniculus* and *S. apella*, which disperse fewer species of plants (Stevenson 2000).

This study provides evidence of the level of complementarity in seed dispersal function that can exist in primate communities and highlights the need to understand primate seed dispersal in the context of the community of dispersers, rather than solely individual species. Additionally, we found that singular traits, such as body mass and degree of frugivory, cannot account for all the variation that exists in seed dispersal function. Individual variation within species due to age and activity patterns can affect the seed dispersal service provided by that species and should be taken into consideration when quantifying seed dispersal function in primates. More comparative research is needed to determine the role of primates as seed dispersers and the implications of their loss on ecosystems.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0266467423000263>

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