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## SEED DISPERSAL OF A PIONEER TREE SPECIES, *CASTILLA ELASTICA*, BY MANTLED HOWLING MONKEYS (*ALOUATTA PALLIATA*) IN REGENERATING FOREST IN COSTA RICA.

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### Introduction

Howling monkeys are well-known seed dispersers for tropical trees (Estrada and Coates-Estrada, 1986; Chiarello and Galetti, 1995; Julliot, 1996), but their importance in general to tropical forest regeneration has been demonstrated for only a few sites (Arroyo-Rodriguez et al. 2015). Studies have demonstrated that both primate species and seedlings of primate-dispersed tree species occur at low densities in forest fragments compared to intact forest areas (Kibale National Park, Uganda: Chapman & Onderdonk 1998), but data on the life history of plants dispersed, excluding basic germination data, are usually lacking. Since howling monkeys (*Alouatta* sp.) are often found in disturbed areas where other primate species are locally extinct, they may be especially important in dispersing seeds in forest fragments where specialized frugivores are absent (Chiarello and Galetti, 1994; Anzués-Dadda et al., 2016).

Seed dispersal requires a number of steps in order to positively affect the reproductive success of the host tree including that passage through an animal's gut does not adversely affect seed germination (Garber and Lambert, 1998). Julliot (1996) found that passage through the gut of a red howler (*A. seniculus*) enhanced seed germination for some species but reduced germination in others. Germination of *Tetragastris panamensis* seeds was not affected by gut passage in *A. palliata* (Howe, 1980). Germination experiments are among the steps needed to assess gut passage effects on seed viability.

General assumptions regarding seed dispersal are that, by moving seeds away from a parent tree, survival is improved by reducing competition among seeds and by reducing competition with the parent tree, and that seedling mortality may be reduced by moving seeds away from areas (such as near the parent tree) that attract seed predators. Seedling survival beneath parent trees also varies between species (Chapman and Chapman, 1995).

Studies of pioneer plant species in Costa Rica showed that the restraints associated with seed dispersal and the reproductive success of plant species vary (Murray, 1986). To

understand the seed dispersal strategy of any species, it is necessary to consider its life history and specific adaptations (Murray, 1986), for example, different pioneer species require different-sized light gaps to permit or stimulate germination. Thus, information on the behavior of potential seed dispersers, as well as on the life histories of host trees, is necessary to understand processes of seed dispersal, and ultimately forest regeneration.

While studying howling monkeys in La Suerte Biological Field Station, Costa Rica in June-July 1997, we found large numbers of seeds of *Castilla elastica* (Family Moraceae) in their feces, deposited more than 25 m from the parent tree. This tree is found from Mexico through Ecuador (Berg 1972). While pioneer tree species usually disseminate a large number of small seeds, *C. elastica*, considered a colonist/pioneer (Berg 1972), has relatively large seeds, about 9-12 mm in length (Estrada, 1993). The guild of dispersers for such a species is less inclusive than for small-seeded pioneer species (e.g., *Cecropia*). Based on these observations, we examined the role of mantled howling monkeys as seed dispersers of *C. elastica*. Specifically, we tested the hypotheses that passage through a howling monkey's gut enhances the germination of *C. elastica* seeds, and that seeds transported away from the parent tree are more likely to survive than seeds deposited beneath the parent crown. To do this we obtained data on (1) experimental seed germination rates, (2) howling monkey feeding and ranging patterns, (3) feeding behavior by potential dispersers on a fruiting *C. elastica* tree, (4) offspring survival beneath parent *C. elastica* trees and (5) the pattern of distribution of adult *C. elastica* trees.

## Methods

La Suerte Biological Field Station (LSBFS) is in the Province of Limón, about 20 km from the Atlantic coast of northeastern Costa Rica [83° 46' 15" W, 10° 26' 30" N]. The site was characterized by areas of secondary, disturbed, lowland rainforest surrounded by cattle pastures and/or crops (pineapple, coconut). Subjects were members of two howler groups living in the "Small Forest" (15 ha). They had overlapping home ranges and were of similar sizes: 11 and 10 individuals (Pruetz and Leason, 2002). We collected data on the distribution of adult *C. elastica* trees, and the survivorship of seedlings beneath the parent trees within the home range of the 11-member group, including the overlap area. Both groups were observed to feed in at least one fruiting *C. elastica* tree in the overlap area. JDP collected data on 98 focal individual feeding bouts during 64.42 group contact hours from May-August 1997. Bouts were defined as the continuous feeding and foraging behavior of an individual, usually within a single tree's crown.

Ninety-five *C. elastica* seeds were planted between 1-20 July, 1997 to assess germination rates under different conditions. We planted 29 seeds voided by howling monkeys, 31 seeds manually cleaned of pulp, and 35 seeds with pulp

intact. Four to five seeds per container were planted on top of a humus and soil mixture within an herbarium slightly shaded by a mesh cover and monitored to record germination. Seedling height was measured in January 1998, 6 months after planting. Of the 95 seeds planted, 23 survived to six months, and mean seedling height was 14.7 cm, ranging from 9-20 cm.

In January-February 1998, we recorded the distribution of *C. elastica* trees in an area representing 10% (1.3 ha) of the Small Forest. We divided the area into 131 quadrats each of 10 m<sup>2</sup> and calculated the mean number of trees per quadrat that were over 3 m in height (considered "immature"). We also collected data on mature trees (Table 1). Those over 9 m tall were considered reproductively mature, since smaller trees were never seen to produce fruit. We measured the occurrence of seedlings, saplings and poles within a 5-m radius from the trunk of the mature trees. Since maximum crown width was 8.5 m (Table 1), a 10 m diameter allowed all seeds deposited beneath parent trees to be recorded. Based on the growth rate of experimentally planted seeds (see above), seedlings over 0.25 m in height were assumed to be from the current year's fruit crop and were recorded as such. From 16-23 July, 1997 a single, large (15 m in height) fruiting *C. elastica* tree in a river-corridor area connecting two forest patches was monitored to record potential seed dispersers (Pruetz *et al.*, 1998). Fruit cover was about 10% of the crown cover during this time. Two-minute instantaneous sampling was used to record the general activity of animals in the tree. The tree was monitored for about 18 h over the course of 8 days, with samples spread evenly throughout the day. The tree was not watched systematically at night, although we saw kinkajous (*Potos flavus*) entering the tree on one occasion.

**Table 1.** Characteristics of the *C. elastica* 'parent trees' surveyed.

Tree Dimension	Mean and SD	Range	Sample Size
Height	12.5 + 1.7 m	9.5-17.0 m	19
Crown width	5.0 + 1.7 m	1.8-8.5 m	19
Girth	0.9 + 0.5 m	0.5-2.5 m	19
Crown height	2.8 + 1.0 m	1.5-4.5 m	19
NN distance*	8.9 + 5.2 m	2.0-17.0 m	15
NN height*	11.6 + 2.3 m	4.5-13.5 m	14

\*NN = nearest neighbor

## Results

Feeding on *C. elastica* fruit accounted for 6% of all howling monkey feeding bouts from May-August 1997. Fifteen birds, three mammals, and two reptiles were also observed to feed on fruit of the focal *C. elastica* tree (Pruetz *et al.*, 1998). Species seen to swallow both pulp and seeds included: the collared aracari (*Pteroglossus torquatus*), keel-billed toucan (*Ramphastos sulfuratus*), mealy parrot (*Amazona farinosa*), iguana (*Iguana iguana*), and the double-crested

basilisk (*Basilisk plumifrons*). Mealy parrots were recorded most often (47% of observation time), with capuchins observed next frequently (19.5% of time). Capuchins (*Cebus capucinus*) were seen to spit seeds, but Smith (2004) noted that they also dispersed *C. elastica* seeds in their feces at LSBFS. Iguanas (6.3% of time), and basilisks (5.1% of time) were also frequent visitors. Howlers did not feed in the focal tree during vigils but were seen there on other occasions.

Thirty-seven *C. elastica* trees between 3 m and 9 m in height were recorded in the 1.3 ha survey area. The high degree of variation (1.21 trees) around the mean number of trees per quadrat (0.28) indicates a clumped distribution of *C. elastica* of this height (Madrigal, 1998). The mean distance to nearest neighbor was 6.08 m (Table 1). ANOVA tests revealed that the number of seedlings, saplings, and poles beneath parent trees did not vary significantly between those that were in light gaps (of at least 10 m<sup>2</sup>) or not (Table 2).

**Table 2.** Mean number of seedlings, saplings and poles within 5 m of adult *C. elastica*.

Tree Location	Height categories (m)						All heights
	0-0.25*	0.26-0.50	0.51-1.0	1.01-2.0	2.1-5.0	>5.0	
<b>Gap</b> (N = 8)	14.4 +22.5	0.8 + 1.0	0.9 + 2.1	0.4 + 0.7	0.3 + 0.5	0.6 + 1.1	17.5 + 25.0
<b>No Gap</b> (N = 11)	12.7 + 15.8	0.7 + 2.1	0.1 + 0.3	0.2 + 0.4	0 + 0	0.4 + 0.7	13.6 + 15.9

\* This year's fruit crop seeds

A Chi-square test using the voided condition to generate expected germination probability (Madrigal, 1998) showed a significant difference in the number of seeds germinating 24 days after planting ( $\chi^2 = 5.00$ ,  $df = 1$ ,  $p < 0.05$ ). Experimental plantings showed that more voided seeds (90%) and manually scraped seeds (87%) germinated sooner than pulped seeds (55%). Time to germination for 50% of all planted seeds (after Julliot, 1996) was shorter for voided seeds (11 days) compared to pulped seeds (19 days) and scraped seeds (18 days). Differences in survivorship to six months under the different conditions (scraped, voided, pulp intact) were not significant and varied from 14% to 34%.

## Discussion

Our experiments showed that passage through a howling monkey's intestinal tract significantly improved the probability of and reduced the latency to germination of *C. elastica* seeds. Ninety percent of the seeds that had passed through a howling monkey's gut germinated, and they germinated more quickly than scraped seeds or seeds with pulp intact. However, scraped seeds also germinated more quickly than seeds with the pulp remaining on them. Zhang and Wang (1995), likewise, found that seeds voided by *Cebus apella* and *Ateles paniscus* did not germinate significantly faster compared to seeds that had been scraped of pulp. Germination for 50 percent of all seeds planted in the current study was slower for both scraped seeds and pulped seeds compared to voided seeds.

The survival of *C. elastica* seedlings beneath parent trees indicates that transport away from a parent tree is not necessary for seed germination in this species. Survival rates tended to be higher in light gap areas than in less open areas in the disturbed forest fragment surveyed here, but the difference was not significant. This finding suggests that *C. elastica* is a pioneer species that can germinate in

small and large gap areas (pattern C in Murray, 1986). However, the distribution pattern of adult *C. elastica* trees implies that most of the offspring beneath parent trees will not survive to reproduce. The nearest-neighbor conspecific distance was greater between mature trees (8.9 m) than between immature trees (6.0 m) (see Table 1), showing that competition between trees is an important factor affecting seedling survival, and thus scattering the seeds away from parent trees is beneficial for this particular pioneer species. Additionally, the number of seedlings below parent trees that were >1 year of age was significantly less than new seedlings, possibly due to high mortality.

Data on the feeding and ranging behavior of howling monkeys in the LSBFS "Small Forest" illustrate that *C. elastica* is an important seasonal food source for howlers at this site (see also Smith 2004). This study and others (Smith 2004) found that howlers ingest and disperse a large number of seeds. Evidence that howlers pass viable seeds, improve the likelihood of germination by passing seeds, and move seeds considerable distances from parent trees supports the hypothesis that these primates contribute to the reproductive success of this tree species.

Data on a focal *C. elastica* tree during a period of high fruit availability showed that, in addition to mantled howling monkeys, other vertebrates such as keel-billed toucans, colored aracarís, iguanas, and basilisks eat the fruits and ingest the seeds and are as such potential seed dispersal agents for the species (Pruetz *et al.*, 1998). Smith (2004) reported that capuchins at La Suerte also swallowed *C. elastica* seeds. The biomass, number of individuals, and behavior of potential dispersers are important variables affecting seed dispersal of fruiting trees. The relative density of howling monkeys is higher than that of capuchins at this site (73 howlers/km<sup>2</sup> vs. 29 capuchins/km<sup>2</sup>; Pruetz and Leason, 2002), as is howling monkey biomass (see Nowak 1999). It is possible that capuchins ingest more *C. elastica* fruits than

do howling monkeys, given their more frugivorous tendencies; however, they were observed to pick seeds from the fruits before eating the pulp, and dropped large portions of whole fruits. Howling monkeys' emphasis on *C. elastica* in their diet – together with their relatively high density at LSBFS – suggest they may be the most important primate seed disperser of *C. elastica* in regenerating forest at this site. Future studies need to detail the feeding behavior of other potential dispersers, if we are to have a clear understanding of the relations between the abundance and distribution of *C. elastica* and its seed dispersers and seed predators. Howe (1980), for example found that mealy parrots destroyed all *Tetragastris panamensis* seeds they eat.

Chiarello and Galetti (1994) noted that howlers are important seed dispersers in isolated forest fragments where specialized frugivores are absent. Pulp removal would seem to be a significant variable affecting seed germination in this tree, and this may also be done by secondary dispersers (for example rodents or ants, see Forget, 1992) that may also play an important role in determining the abundance and distribution of *C. elastica* in the forest fragments of La Suerte. Overall, dispersers depositing seeds in gaps, away from other trees, undoubtedly contribute to forest regeneration, but the precise relation between forest structure and composition and the role of primates is one of the key questions to be answered in understanding their “ecological services” for the maintenance of healthy forest functioning and their conservation.

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## IMMIGRATION OF A FEMALE *ALOUATTA GUARIBA CLAMITANS* INTO A GROUP INHABITING A RESTINGA FOREST IN SOUTHERN BRAZIL

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### Introduction

Among primates, dispersal may result from aggressive interactions (competition for reproductive positions, social status or food resources) or from a result of events such as changes of social hierarchy, infanticide avoidance, fission of a group or habitat destruction (Pusey and Packer, 1987). Although there are benefits attributed to primate dispersal (increased genetic variability, reduced inbreeding and possibly diminished competition for reproductive opportunities), predation risk increases and the chances of finding food and familiarity with the environment decrease when an individual disperses (Chepko-Sade *et al.*, 1987; Pusey and Packer, 1987; Shields, 1987; Jones, 2005). Additionally, arboreal primates face high costs for traveling in open anthropic areas to reach other forest fragments (e.g., predation, morbidity associated with automobile, illegal trade) (Rodríguez-Toledo *et al.*, 2003; Mandujano *et al.*, 2004). The relations between intrinsic factors (social, demographic and genetic) and habitat factors (deforestation, hunting and others) that influence the decision of an individual to stay or leave its natal group are complex and may vary among species and sexes (Mandujano *et al.*, 2004; Jones, 2005).

Female philopatry is common among primates (Pusey and Packer, 1987) but Neotropical primates polygamist species tend to a female-biased dispersal (e.g. *Brachyteles hypoxanthus* and *Ateles chamek*) or bisexual dispersal (e.g. *Cebus olivaceus*, *Leontopithecus rosalia* and *Saguinus fuscicollis*) (Campbell *et al.*, 2007; Strier, 2008). For howler monkeys, the dispersal of both males and females has been observed in *Alouatta palliata* (Glander 1992; Jones 1980, 1999; Mandujano *et al.* 2004, Clarke and Glander, 2008), *Alouatta seniculus* (Rudran, 1979; Crockett, 1984; Crockett and Pope, 1993; Agoramoorthy and Rudran, 1993; Palacios, 2000; Pope 2000), *Alouatta caraya* (Rumiz, 1990; Calegario-Marques and Bicca-Marques, 1996; Giudice, 1997), and *Alouatta pigra* (Brockett *et al.*, 2000). For *Alouatta guariba clamitans* some cases cited in the ecological studies report the dispersal of howlers, mostly adult and sub-adults males (Mendes,

- 1989; Katz and Otta, 1991; Strier *et al.*, 2001; Jardim, 2005; Miranda *et al.* 2006; Podgaiski and Jardim, 2009).

### Methods

Ten groups of howler groups (*Alouatta guariba clamitans*) (Cabrera, 1940) were monitored as part of a study of population ecology (Jardim, 2005) in three forest fragments around the cities of Porto Alegre and Viamão in state of Rio Grande do Sul: Lami (300 15' S; 510 03 W); Morro da Extrema (30012' S; 510 04 W) and Parque Estadual de Itapuá (30o 23' S, 51o 30' W). The determination of the group composition was conducted according to the age–sex classification used for *A. g. clamitans*, in Caratinga, Minas Gerais (Mendes, 1989). Howlers were individualized mainly by body size, pelage color and scars. After the initial definition of the social composition (from June to November 1999), the howler groups were followed every second month from December 1999 to December 2001.

Thirteen surveys were carried out and the following information was registered: date, time, location, and social composition of each group. Every change in group composition due to births, deaths, and dispersal was documented as the group was encountered. The groups were observed by the method *ad libitum* (Altmann, 1974) for at least two hours at each encounter. The average interval between the surveys was 50.2 days, with a total of 149 days on-site (586 hours of direct observation) and 214 encounters with groups of howler monkeys.

### Results

On February 16, 2000, we recorded the immigration of an adult female into a resident group in a Restinga forest fragment in Lami, a private property in Porto Alegre. This group originally contained eight individuals (two adult females, one adult male, four juveniles, and one infant). This same composition was observed in three surveys previous to immigration. When the group was first seen with the new female, we made the following observations: the immigrant female, while vocalizing, moved towards one of the resident adult females, which moved away, apparently showing submission. The second female was carrying an infant on her back and was about 50 meters from the rest of the group. The male was seemingly indifferent to the females' behavior. In the following months, no aggressive behaviors or displays of domination–submission among the females were observed. Similarly, aggressive behavior was not observed among females in the same group in other groups observed. Agonistic interactions were always observed between females of different groups in the context of intergroup conflicts. In July 2001, approximately 18 months after her arrival, the immigrant female gave birth. Throughout the survey, there was no other alteration of the social composition of this group, except for four births. In the other groups,