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Source: Tropical Conservation Science, 2(3) : 266-281

Published By: SAGE Publishing

URL: https://doi.org/10.1177/194008290900200301

Research Article

The Fate of Seeds Dispersed by Golden Lion Tamarins (*Leontopithecus rosalia*) in an Atlantic Forest Fragment, Brazil

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Abstract

Frugivores, as seed dispersers may influence the spatial patterns of adult and juvenile plants, but a large portion of the potential recruitment of plant populations is lost to seed predators. The majority of seeds dispersed by primates are killed by seed predators or moved by secondary dispersers. Little is known about post-dispersal seed-predation and seedling distribution of exploited plant species. This study iinvestigated the survival and establishment of seedlings from seeds defecated by the golden lion tamarin (*Leontopithecus rosalia*), a frugivorous endemic primate of the Atlantic Forest of Brazil. Two groups of golden lion tamarins were studied in the União Biological Reserve from April 2003 to March 2004. Seeds from fruits consumed by tamarins and collected from their feces were evaluated with respect to the following: germination success, seed disappearance or secondary dispersal on the forest floor, seed predation, and seedling establishment and survival for the length of the study period. The tamarin groups consumed 88 fruit species. Of these, 38 were used to run 107 experiments which indicated that more than 50% of the seeds disappeared, about 15% died before germinating and seeds of 22 species reached the seedling stage. At the end of the study, only 15 of these species still had surviving seedlings. Studies on seed fate are important for understanding the role of the golden lion tamarind in the natural process of forest regeneration in the lowland Atlantic Forest of the state of Rio de Janeiro in Brazil.

Key Words: germination, seed predation, secondary dispersal, golden lion tamarin, *Leontopithecus rosalia*.

Resumo

Animais frugívoros, como dispersores de sementes, podem influenciar os padrões espaciais de plantas jovens e adultas, mas uma grande parte do recrutamento potencial de populações vegetais é perdida para os predadores de sementes. A maioria das sementes dispersadas por primatas nas florestas é morta por predadores de sementes ou movida por dispersores secundários. Pouco se sabe sobre a predação de sementes pós-dispersão e a distribuição das plântulas das espécies exploradas. Esta pesquisa é a primeira a considerar a sobrevivência e estabelecimento das plântulas provenientes de sementes defecadas por micos-leões-dourados (*Leontopithecus rosalia*), espécie de primata frugívoro e endêmico da Mata Atlântica, estudando a importância destes como dispersores de sementes. Dois grupos de micos-leões-dourados foram estudados na Reserva Biológica União de abril de 2003 a março de 2004. Sementes dos frutos consumidos pelos micos e coletadas nas suas fezes foram avaliadas no que se refere à germinação, desaparecimento ou dispersão secundária, predação, mortalidade ou sobrevivência, e estabelecimento das plântulas. Durante o período de estudo os grupos de micos consumiram 88 espécies de frutos, e 107 experimentos foram conduzidos com sementes de 38 espécies de frutos. Mais de 50% das sementes desapareceu durante os experimentos, e cerca de 15% morreu antes de germinar. Sementes de 22 espécies sobreviveram até o estágio de plântulas, mas no final do estudo, somente 15 dessas espécies ainda apresentavam plântulas sobreviventes. Estudos sobre o destino das sementes são importantes para a conservação dos micos-leões-dourados e seu habitat, a Mata Atlântica de baixada costeira do estado do Rio de Janeiro, um dos mais ameaçados ecossistemas do mundo.

Palavras-chave: germinação, predação de sementes, dispersão secundária, mico-leão-dourado, *Leontopithecus rosalia*.

Received 5 December, 2008; Accepted 28 January, 2009, Published: 10 August, 2009

Cite this paper as: Lapenta, M. J. and Procópio-de-Oliveira, P. 2009. The Fate of Seeds Dispersed by Golden Lion Tamarins (*Leontopithecus rosalia*) in an Atlantic Forest Fragment, Brazil. *Tropical Conservation Science* Vol.2 (3):266-281. Available online: www.tropicalconservationscience.org

Introduction

In tropical forests, 45-90% of tree species produce fleshy fruits suitable for consumption by birds and mammals [1]. Mammals, like other frugivores, either ingest the fruit pulp and spit the seeds out, pass them through the gut, or digest them [2].

Frugivorous animals may influence the spatial patterns of young and adult plants, promoting seed shadows around the parental tree due to viable remnant seeds dispersed near the parent tree [2,3]. The seed shadow generated by primary dispersers is often modified by secondary dispersers and post-dispersal predators [4]. A large portion of a plant population's potential recruitment is lost to seed predation, and this is the main ecological and evolutionary force that affects trees at the individual, population, and community levels [4].

Many studies show the important role of ants and dung beetles in secondary seed dispersal, as they remove and bury seeds defecated by primary dispersers, making it more difficult for rodent predators to find the dispersed seeds [5-10]. Some post-dispersal rodent predators may act as secondary dispersers as well, burying the seeds that have escaped predation by other species. These seeds may germinate if forgotten by the rodents [11-15]. In addition, the sites where the seeds are deposited by secondary dispersers may be more appropriate for their establishment and survival than the site of primary dispersal.

The golden lion tamarin (*Leontopithecus rosalia*) is an endemic primate to the Coastal Atlantic Forest and feeds on a variety of invertebrates, small vertebrates, bird eggs, and fruits [16-17]. The fruits most frequently consumed by the tamarin are pulpy, sweet and soft [18]. The majority of fruits are yellow, followed by black and purple[19]. These primates additionally feed on exudates, unripe fruits, and flowers [17, 20]. In general, the tamarins swallow elongate seeds and spit round seeds. The mean seed length and width of swallowed seeds are, respectively: 13.0 mm and 7.8 mm; and of spit seeds are, respectively: 13.4 mm and 10.4 mm [17]. Preservation of golden lion tamarin habitat is one of the greatest obstacles for the conservation of this species. The tamarins habitat: the Coastal Atlantic Forest in the state of Rio de Janeiro [21], is one of the most endangered ecosystems in the world [22].

The first systematic and long-term study of the golden lion tamarins role as seed dispersers considered them to be legitimate dispersers (*sensu* Reid [23]) based on the germination of ingested seeds, even in low percentages, in tests performed in the lab and in the field [24]. Beside germination viability, the golden lion tamarins are important for other aspects of seed dispersal, such as dispersal distance and place of seed deposition [25].

Our study represents a continuation of studies on primary seed dispersal and germination in the lab [24, 26], and of some aspects of the effectiveness of the golden lion tamarins as dispersers [25]. In this study, we observed the fate of seeds dispersed by golden lion tamarins. This is the first study to consider the

secondary effects of dispersal by these small primates, for many fruit species.

The conservation of the ecological associations in which primates participate are of fundamental importance in sustaining their habitat [27] and has taken on a degree of urgency, due to the recent decline of many frugivore populations [28].

The objectives of this study were: 1) to determine the rate of mortality or seed disappearance by predation and/or secondary dispersal of seeds defecated or spit out by golden lion tamarins compared to seeds taken directly from fruits; 2) to investigate, when possible, the primary secondary dispersers and/or predators of seeds defecated or spit out by the golden lion tamarins; 3) to verify if seeds defecated or spit out by tamarins have a higher probability of germination and seedling establishment than seeds taken directly from fruits, and investigate the establishment and survival of these seedlings.

Methods

Study site

The study was conducted in the União Biological Reserve (UBR; 22°27'36"S, 42°02'15"W), located in the municipalities of Rio das Ostras and Casimiro de Abreu, in the state of Rio de Janeiro, Brazil (Fig. 1). The UBR, administered by the Brazilian Institute for the Environment (IBAMA) consists of 3,121 ha with 2,400 ha of forest, divided into two sections by Federal Highway BR 101.

The population of golden lion tamarins in the União Farm was formed in 1994 by the translocation of six groups (42 individuals) of tamarins from forest fragments [29-30]. Despite being located within the natural range of the species, no native golden lion tamarin population existed in this area in 1994. In 1998, the Farm was transformed into the União Biological Reserve, protecting the new golden lion tamarin population, currently formed by 220 individuals distributed in 30 groups in the Reserve [17].

Together with *L. rosalia*, other frugivorous animals occur in the UBR: capuchin monkeys (*Cebus nigritus*), howler monkeys (*Alouatta guariba*), squirrels (*Sciurus aestuans*), South American coati (*Nasua nasua*), kinkajou (*Potos flavus*), tayra (*Eira barbara*), crab-eating fox (*Cerdocyon thous*), bats, rodents, marsupials and many frugivorous birds [25].

The climate in the region is hot and humid with a defined seasonality. The dry season occurs from April to September, and the wet season from October to March. The mean annual rainfall was 1,876 mm during the study period, with maximum temperature averaging 27.6 ± 2°C and minimum temperature averaging 19.5 ± 2.5°C. Kierulff [21] distinguished three types of vegetation in the UBR, based on topography and drainage systems: 1) SWAMP FOREST, flooded areas with open canopy, high liana density, and a dense understory; 2) LOWLAND FOREST, seasonal flooding and numerous epiphytes; and 3) HILL FOREST, low epiphyte density, and dense canopy cover. These characteristics were used to determine if the golden lion tamarins defecated seeds in the same habitat where the adult trees are distributed [25].

Frugivory and primary seed dispersal

Two previously habituated groups of golden lion tamarins were each followed from dawn until dusk (from sleep site to the consecutive sleep site) three days per month from April 2003 to March 2004. The SJ2 group (8 to 13 individuals), translocated in 1996, was followed for 412 h. The Geni group (7 to 13 individuals), formed in the UBR in 1998 and was followed for 300 h.

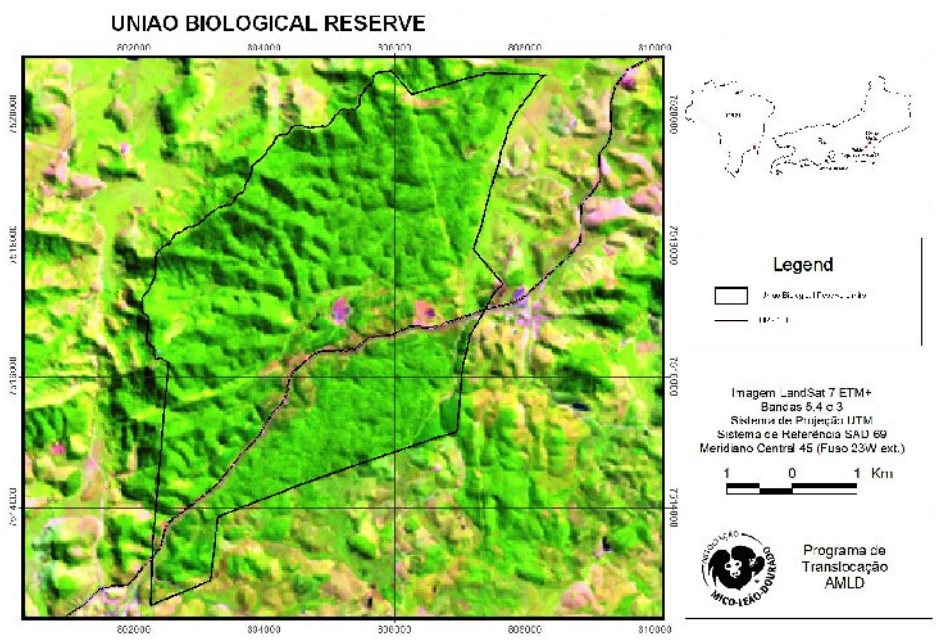

Fig. 1. Location of the União Biological Reserve, State of Rio de Janeiro, Brazil. Pink patches: urban places; Green patches: forest.

The data were collected specifically to obtain information on fruit feeding and seed dispersal (how many times the tamarins fed on fruits or deposited feces containing seeds), and were pooled together for analysis. Trees that were used by the tamarins as a fruit resource were marked with numbered flags, and the portion of fruit consumed and the fate of the seeds (spit, ingested, or destroyed) were noted. Samples of fruits eaten by the tamarins were collected and the weight and size of the seeds were recorded. To calculate the size of the seeds we multiplied the length by the width of the seed.

Feces were collected immediately after defecation from all group members, and the defecation sites were marked by flagging tape tied above the forest floor. The number of seeds in the feces that were greater than 3mm in length was counted. These seeds were then returned to the site from which they were collected for seed-fate experiments the following day.

Seed-fate experiments

The seed-fate experiments were conducted in the field with 32 plant species whose seeds were consumed by golden lion tamarins. For the 24 plant species whose seeds were ingested, the experiments were performed with seeds from feces (treatment) and with the same number of seeds directly taken from fruits (control). For the eight plant species whose seeds were not ingested by the tamarins, the experiments were performed with seeds that had been spit out by tamarins (treatment) and seeds taken from inside the pulp (control).

In the experiments we used the same number of seeds defecated or spit out by the tamarins (but without fecal material or fruit pulp and without any previous washing). The leaf litter was removed from the experimental sites to allow for observation of seed disappearance, predation or germination. The experiments were checked once a week in the first month, and after that, at intervals of one month until the end of the study (until March 2006) to verify the number of seeds removed, preyed upon, surviving, or germinated, and to monitor establishment of the seedlings. The fate of control and treatment seeds in the forest was compared.

Data analysis

We used a Chi-square test (Yates correction for n < 200; degrees of freedom = 1; [31]) to compare seed disappearance and mortality of control and treatment seeds. The number and the size of the seeds were both correlated with percentages of seed disappearance and mortality. The germination of treatment and control seeds, and the development until seedling stage, in the two categories, were compared using the Chi-square test.

We used Correspondence Analysis (Statistica 6.0), with data on germination, seed disappearance, and mortality to verify which characteristics of seeds and feces deposition influenced the fate of the control and treatment seeds. The scores of the units on the first two axes were correlated with the number of seeds in the experiments, weight and size of the seeds (length versus width), the distance of dispersal (by Pearson Correlation), and to the habitat of seed deposition using One–way ANOVA (for the distance and habitat of deposition we only used the scores that corresponded to treatment seeds). In a previous study we measured the dispersal distances for all species, using trees and feces deposit position located on a map of the area (only when we were certain of the parent tree). For the habitat of deposition we tested whether the distribution of feces across habitat types HILL, LOWLAND, and SWAMP, was significantly different from that of the feeding trees across habitat, for each tree species. (for complete data see Lapenta and Procópio-de-Oliveira [25]).

Results

Frugivory and primary seed dispersal

During the study period, the two tamarin groups consumed a total of 88 species of fruits from at least 18 plant families.

During the feeding, the tamarins ingested the seeds of 43 species (48.9%) and spit out the seeds of 45 species (51.1%). The seed size of the consumed fruits varied from less than 3 mm to 20 mm in length (Table 1). The small seeds (less than 3 mm in length) were always ingested by the golden lion tamarins, while the large seeds were spit out.

During the study period, we collected 340 fecal samples containing seeds from 41 plant species. From these fecal samples, 255 samples, representing 34 plant species, contained 875 seeds > 3 mm.

Seed fate experiments

We used 32 species of seeds from the fruits consumed by the tamarins in the seed-fate experiments. We present data for 28 plant species for the seed disappearance and mortality experiments, and provide data for the 22 plant species that germinated.

During the study period, 53.1% of treatment seeds (329 seeds) and 49.7% of control seeds (310 seeds) disappeared in seed-fate experiments. These seeds were preyed upon or removed by secondary dispersers (Table 1). Of the 19 species with seeds ingested and defecated by the tamarins, 42.1% (eight species) had an equal seed disappearance of treatment seeds (from feces) and control seeds (from fruits). Seed disappearance was highest for five species of treatment seeds (26.3%) and for six species of control seeds (31.6%). Among the eight species with seeds spit out by tamarins, Unknown 11 and Myrtaceae sp.3 (25%) showed an equal seed disappearance between treatment (spit seeds) and control seeds (seeds with pulp) (Table 1). Seed disappearance was highest for four species of spit seeds (50%) and in two species with pulp (*Eugenia robustovenosa* / Myrtaceae and *Paullinia ferruginea* / Sapindaceae).

Seed disappearance in the field was not related to seed size (length versus diameter; n = 28; r = 0.08; p = 0.68), but was highly correlated with the number of the seeds used in the experiments (n = 70; r = 0.52; p < 0.001 and n = 69; r = 0.59; p < 0.001, respectively).

At the end of the study, 115 treatment seeds (18.5%) and 132 control seeds (21.1%) died before

germinating.

Among the 14 species of plants with seeds ingested and defecated by the tamarins, seven (50%) showed similar mortality for treatments and control (Table 1). Seed mortality was higher for five species of plants collected from feces (35.7%) and for the seeds from fruits in 14.3% of the plant species (Unknown 7 and *Inga thibaudiana*). Of the seven species of plants with seeds spit out by the tamarins, 42.9% (*Eugenia robustovenosa*, *Eugenia* sp.4, Myrtaceae sp.3) experienced similar mortality for control (with pulp) and treatment seeds (spit out) (Table 1). The mortality was higher for seeds with pulp in 57.1% of the species (*Eugenia* cf. *excelsa*, *Eugenia* sp.1, Myrtaceae sp.1 and Unknown 11). The mortality of the seeds in the field was positively correlated with their size (n = 28; r = 0.47; p = 0.012).

Table 1. Percentage of disappearance and/or mortality between control seeds (from fruits, or seeds with pulp) and treatment seeds (from feces or spit out) in the União Biological Reserve, RJ-Brazil. Seed size = length / width (mm) * species with spit seeds.

Species	Seed size	Nº seeds treatment/ control	% disappearance				% mortality			
			Treat-ment	control	χ^2	p	Treat-ment	control	χ^2	p
Rollinia dolabripetala	7.3 / 0.6	89 / 89	100	98.9	0	ns	0	0	-	-
Pourouma guianensis	17.2/8.3	10 / 10	70	100	4.9	< 0.05	0	0	-	-
Euphorbiaceae sp.1	8.4/6.5	10 / 10	10	30	9.0	< 0.01	60	50	0.74	ns
Inga edulis		57 / 57	80.7	64.9	1.50	ns	19.6	33.33	3.06	ns
I. thibaudiana		33 / 33	69.7	63.6	0.19	ns	0	36.4	34.43	<0.001
I. sp.2	17.5/10.1	6 / 10	66.7	0	64.71	<0.001	0	0	-	-
Helicostylis tomentosa	7.9 /7.25	6 / 6	0	50	48.02	< 0.001	100	50	16.01	<0.001
Calycorectes sp.1	7.7/6.7	44 / 44	29.5	22.7	0.64	ns	6.8	2.3	1.35	ns
*Eugenia robustovenosa**		18 / 18	0	16.7	14.8	< 0.001	72.2	66.7	0.15	ns
E. cf. *excelsa**		11 / 11	81.8	18.2	39.2	< 0.001	18.2	81.8	39.2	<0.001
E. sp.1*	12.5/14.3	10 / 10	20	0	18.0	< 0.001	30	50	4.51	<0.05
E. sp.4*		25 / 25	28	8	10.03	< 0.01	60	52	0.44	ns
Marlierea sp.1		12 / 12	0	0	-	-	33.3	50	2.96	ns
Myrcia fallax	8.1/3.6	6 / 6	83.3	83.3	0	ns	0	0	-	-
Myrtaceae sp.1*	7.3/8.4	30 / 30	33.33	10	11.51	< 0.001	26.7	46.7	4.92	<0.05
Myrtaceae sp.3*	17.6/14.25	7 / 7	42.9	28.6	2.47	ns	57.1	71.4	1.38	ns
Myrtaceae sp.11		14 / 14	7.1	0	5.24	<0.05	7.1	14.3	1.78	ns
Guapira opposita		4 / 4	50	75	4.61	<0.05	25	0	23.04	<0.01
Passiflora rhamnifolia		22 / 22	100	100	0	ns	0	0	-	-
Randia sp.1	11.4/9.0	31 / 31	48.4	51.6	0.05	ns	22.6	6.45	7.9	< 0.01
Tocoyena brasiliensis	12.4/10.5	35 / 35	37.1	68.6	8.8	<0.01	17.1	2.9	8.71	<0.01
*Paullinia ferruginea**	9.6/9.4	11 / 11	0	18.2	16.25	< 0.001	0	0	-	-
Micropholis guyanensis		7 / 7	42.9	71.4	6.62	= 0.01	57.1	28.6	8.82	<0.01
Pouteria bangii	20/11.4	24 / 24	41.7	20.8	6.34	< 0.05	29.2	29.2	0	ns
Sarcaulus brasiliensis	15.5/9.1	88 / 88	44.3	46.6	0.02	ns	15.9	13.6	0.06	ns
Unknow 7	13.8/7.2	4 / 4	75	25	24.0	< 0.001	25	75	24.01	<0.001
Unknow 11*		4 / 4	25	25	0	ns	0	25	23.04	<0.01
Unknow 18		2 / 2	50	0	48.0	< 0.001	0	0	-	-
TOTAL		**620 / 624**	**53.1**	**49.7**	**0.06**	**ns**	**18.5**	**21.1**	**0.06**	**ns**

It was not possible to identify the predator or dispersal agent for the majority of the seeds that disappeared or were preyed upon. Nevertheless, in some cases we observed the presence of ants or beetles, or found signs of these insects (holes) or of mammals (bite-marks). The action of predators and/or secondary dispersers was similar between treatment and control seeds, but the ants were the most frequent group in number of experiments as well as number of species and seeds visited.

Evidence of beetle atacks was found in the experiments with eight species (Table 2). In some of these experiments, the seeds had holes made by beetles, but were still viable for germination. Ants atacks were found in experiments with 12 species and evidence of mammal predation was found in seeds of five species.

Table 2. Seed species with evidence of beetles, ants or mammal atacks.

Species	Beetles	Ants	Mammals
Rollinia dolabripetala		x	
Cecropia pachystachya		x	
Cecropia hololeuca		x	
Pourouma guianensis		x	
Euphorbiaceae sp.1			x
Inga thibaudiana	x	x	x
Inga sp.2		x	
Miconia cinnamomifolia		x	
Hyperbaena domingensis		x	
Helicostylis tomentosa		x	
Eugenia robustovenosa	x		
Eugenia sp.1	x		
Myrtaceae sp.1			x
Myrtaceae sp.3	x		
Passiflora rhamnifolia	x		
Randia sp.1		x	
Tocoyena brasiliensis			x
Pouteria bangi	x	x	
Sarcaulus brasiliensis	x		x
Unknown 7	x	x	
Total species	**8**	**12**	**5**

For the germination tests we considered the number of seeds available at the momment of the first germination and not at the beggining of the experiment (excluding the seeds that disappeared or were preyed upon before germination began). Appendix 1 shows the results of the 22 germinated species. In total, 137 treatment seeds (from feces or spit; 53.5%) and 157 control seeds (from fruits or seeds with pulp; 57.3%) germinated, but there were no significant differences in germination for control and treatment seeds.

When we focused on species of plants (the majority of the results for the species with more than one test), only *Eugenia robustovenosa* showed a higher germination for treatment seeds (5.9%). Three species had a higher germination of control seeds (17.6%), eight species presented no significant differences in germination (47.1%), and tests with five species had conflicting results (29.4%).

In 36 experiments, the treatment of the seeds by golden lion tamarins resulted in significant improvement in germination in only three tests with spit seeds (8.3%) and in four tests with ingested and defecated seeds (11.1%). The treatment by golden lion tamarins decreased the germination in 14 tests with ingested seeds (38.9%) and in one test with seeds inside fruit pulp (2.8%). In 14 tests, the difference in germination was not significant (11 tests with ingested seeds (30.6%) and three tests with spit seeds (8.3%)).

The rates of seed disappearance, mortality and germination were similar between the treatment and the control seeds, but in total, the percentage of seeds that disappeared was higher than the percentage of seeds that died or germinated (Fig. 2).

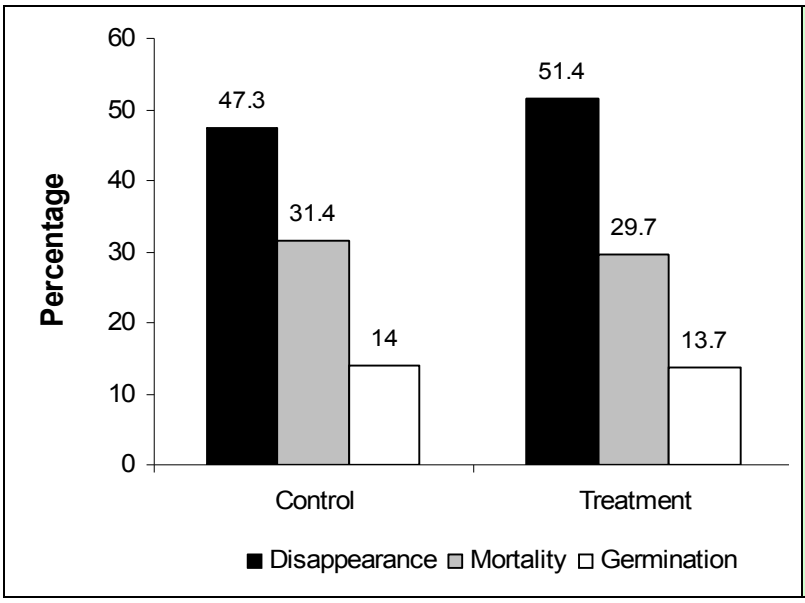

Fig. 2. Percentages of seed disappearance, mortality and germination of control and treatment seeds in the União Biological Reserve, RJ-Brazil.

Seventy-one percent of the variance was explained by the first two axes in a correpondence analysis containing the variables seed disappearance, germination, and mortality. The first axis positioned the variables seed disappearance and germination in opposite corners, and explained 56.5% of the variation. The second axis illustrated polarization between mortality and germination.

The distance and the habitat of seed dispersal are not correlated with the first two axes (disappearance and germination and mortality and germination, respectively). The number of seeds in the experiments is correlated with the second axis ($r = 0.205$; $p < 0.05$; $n = 143$), showing a tendency for increasing mortality with increasing number of seeds in the experiments. The weight of seeds, as is their size (length versus diameter), is correlated with the first axis ($r = 0.36$; $p < 0.01$; $n = 118$ and $r = 0.26$; $p < 0.05$; $n = 82$, respectively), with a tendency for improved germination with increasing weight or size of the seeds.

Seedling establishment

The 22 germinated species developed seedlings (92 treatment seeds and 117 control seeds) (Appendix 1) but the results were not statistically different when the two groups were compared.

When we focused on species of plants used in the experiments (considering the majority of the results for the species with more than one test), only *E. robustovenosa* showed a higher percentage of seedlings sprouting from treatment seeds (5.9%), and Euphorbiaceae sp.1 a higher percentage of seedlings sprouting from control seeds (5.9%). For the majority of the species, there were no significant differences in seedling development (12 species; 75%), and for two plant species, the results of the tests were conflicting (12.5%).

Of the 25 tests performed, only one with spit seeds (4%) and one with ingested and defecated seeds (4%) showed improved development of germinated seeds into seedlings as a result of having been manipulated by or passed through the gut of the golden lion tamarins; and in four tests with ingested seeds (16%), the treatment by tamarins was found to decrease the percentage of seedlings that emerged. In 19 tests, the

difference in seedling development was not significant (15 tests with ingested seeds (60%) and four tests with spit seeds (16%)).

At the end of the study, only 15 of these species had surviving seedlings (52 seedlings from treatment seeds, 73%; and 54 seedlings from control seeds, 71.05%).

The difference between survival of seedlings in the two categories was not significant ($\chi^2 = 0.01$; $p > 0.05$).

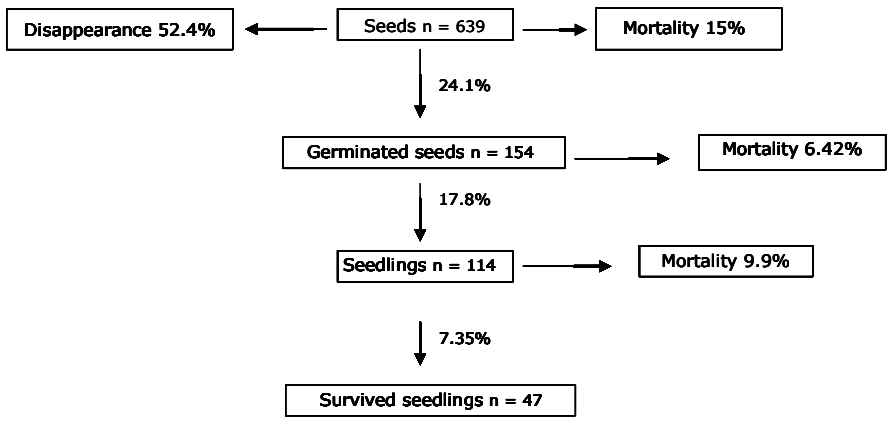

Fig. 3. Diagram of seed fate in control experiments in the União Biological Reserve, RJ-Brazil.

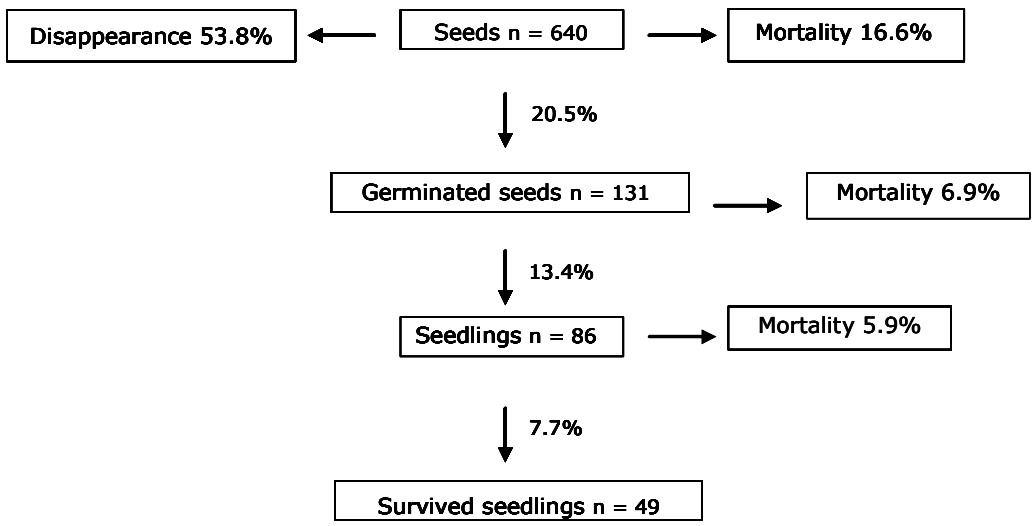

Fig. 4. Diagram of seed fate in treatment experiments in the União Biological Reserve, RJ-Brazil.

Seed fate diagrams

The survival of the seeds at the end of the study (considering all the seeds at the begining of the experiment and observed throughout the study period to check seed disappearance, mortality, germination, and appearance of seedlings) was similar between the experiments with control and treatment seeds (Figs. 3 and 4). More than half of the control and treatment seeds left to germinate in the field disappeared. The percentage of germination of seeds and of seedlings was higher than the percentage of mortality in control experiments. In the experiments with treatment seeds, the percentage of mortality was higher in seeds than in seedlings, but mortality of seedlings in control experiments was higher. At the end of the study, 7.35% of seedlings from control seeds and 7.7% of seedlings from treatment seeds were surviving.

Discussion

We examined the fate of seeds dispersed by golden lion tamarins (Fig.5) in União Biological Reserve. A seeds' arrival is only the first step in the process of tree establishiment. Many factors in the post-dispersal process alter recruitment after the arrival of the seeds [32], and this represents one of the most complex phases of seed dispersal. These processes include many variables, such as morphological characteristics of seeds and frugivores, temporal variations of food availability, habitat and microhabitat where seed deposition occurs, microclimatic needs, and many others.

The majority of golden lion tamarin feces were deposited on leaf litter. The removal of the leaf litter in our experiments facilitated and increased the percentage of predation or secondary dispersal of the seeds. However, the litter was removed in both control and treatment experiments to avoid biases across treatments.

Seeds defecated singly without fecal matter have a greater chance of avoiding detection by rodents and insect predators [33]. Seeds enveloped by fecal material may be more easily located by granivores, diminishing the survival chances of species that need to germinate quickly. The influence of organic material on location of the seeds diminished over time [34]. However, seeds defecated by the golden lion tamarins are enveloped in little organic material [25], which may explain the similar seed disappearance among the control and treatment seeds. In this study, seed disappearance was not related to the size of the seeds when all plant species were considered. The tamarins did not ingest large seeds, and we used control seeds with pulp in the experiments for these seed size category. The higher rate of seed disappearance among treatment seeds may be due to the preferences of secondary dispersers who prefer the seed to the fruit pulp as a food resource. The small secondary dispersers and/or seed predators may be attracted by the smell of the feces, but preferred the seeds from fruits as a food resource. The rate of removal by insects is sometimes underestimated, because seeds may be considered as having been preyed upon when they were only removed by secondary dispersers and buried in other places.

When all species of seeds were pooled together, the rate of mortality was correlated with seed size. In large seeds, the rate of mortality was higher for control seeds (seeds with pulp), probably due to fungi and pathogens. In this way, the golden lion tamarin is acting as an efficient disperser for many plant species even without ingesting the seeds due to the decreased mortality of the ingested or spit seeds, allowing the seeds to survive and germinate. Seeds spit out by chimpanzees also show a higher rate of germination than seeds from fruits fallen on the forest floor without ingestion [35]. In the absence of large frugivores to ingest and disperse large seeds the seed-spitting may be an effective means of seed dispersal for large-seeded tress [36-37]. The majority of studies on seed dispersal consider only the importance of seeds ingested by frugivores. Nevertheless, studies focusing on the handling of fruits and seeds by frugivores cannot be neglected if our aim is to increase understanding of their role in the dispersal and establishiment of seedlings.

Many predators may respond to distance of seeds deposition in relation to parental tree, and density of

the seed pile, depending on the season, availability of alternative resources, and relative density of young plants [38]. In this study, the number of seeds used in the experiments is highly correlated with their seed disappearance in the field. The correlation between the size and the weight of seeds and the scores of the experiments show a tendency toward increasing mortality with higher number of seeds. Thus, in the experiments with many seeds, after the seeds have disappeared, there is a higher tendency for mortality than germination. The large seeds are not ingested and are spitted out by the tamarins, but these seeds are benefited in germination, due to the remove of the pulp.

In the present study, seed disappearance, germination, and mortality of seeds were not influenced by the distance between the parental tree and the place of seed deposition and habitat of dispersal. Nevertheless, these factors are very important in the process of seed dispersal and should be considered [25]. The results presented about the habitat and distance of seed dispersal may be related to the methods used, which did not take into consideration the distribution of other trees of the same species near the site of feces deposition. In addition, we used the average dispersal distance for each seed species, and not the distance of the seeds used in each experiment. In the tests performed, we considered the habitat of feces deposition, but the plant species may be distributed and had the seeds germinating in more than one habitat [25].

We found no significant differences between germination of treatment seeds (defecated or spit out) and control seeds (from fruits or seeds with pulp) in the majority of tests (38.9%). In a previous study of seed germination in the lab, no significant differences in germination of seeds ingested and defecated by the golden lion tamarins were found in about 50% of the tests. These results varied with the plant species, and in experiments with the same plant species carried out in different periods [24, 26].

The number of seeds used in the tests (seeds per experiments) was low because we used the actual number of seeds found on tamarin feces. A portion of these seeds were preyed upon or removed by secondary dispersers before germination, decreasing the number of seeds available in the experiments. The lack of correlation between the number of seeds used in the tests and the number of seeds that germinated may be due to the relatively low number of the seeds.

Other studies on seed dispersal by primates have not found a consistent effects on percentage or velocity of germination because some seed species were benefited while others were harmed [39-42].

In addition to the role of the frugivore, many abiotic factors not considered in this study may influence germination, according to the needs of each plant species: temperature band specific to each species; light conditions (degree of canopy ovelap, edges, terrain configuration); moisture; and presence or absence of litter [25, 43].

Seed germination may be benefited by the actions of secondary dispersers due to the transport of seeds to places more propitious for germination and establishment, and more protected from harmful attacks by seed predators. According to Voysey *et al*. [44], the transition from seed to established seedling is the most vunerable phase on the life cycle of a plant. In this study, the majority of germinated seeds developed into seedlings (73% of treatment seeds and 71.05% of control seeds (Fig. 5)), showing that the first obstacle faced by seeds that survive predation is to find favorable conditions to germinate. Pizo [45] also found higher mortality among seeds from Myrtaceae species (65.2%) in comparison with the mortality of seedlings from the same species (12%), caused by removal and predation by rodents.

Survival of seedlings and seeds was similar in this study, with about 50% of seedlings surviving at the end of the study. The seedlings used in this study will face additional obstacles in the survival to the adult phase and these obstacles must be considered in other long term studies. Nevertheless, with our data, we concluded that seeds with fast germination, like *Inga* spp. and species from the Myrtaceae family [25] escaped mortality and developed into seedlings. Many seedlings from the Myrtaceae family were still surviving at the end of the study, including the ones from seeds spited out by the tamarins.

Fig. 5. Upper photo: golden lion tamarins in the Atlantic Forest, Brazil. Photo © L Candisani. **Bottom photos:** species with developed seedlings in the União Biological Reserve. (a) *Inga edulis*, (b) *Eugenia* sp.1, (c) Unknown 18. Photos © MJ Lapenta.

Implications for conservation

Golden lion tamarin feeding behaviour and foraging patterns stresses their role as seed dispersers in the Atlantic Forest. They disperse large numbers of seeds, time of seed retention in the gut is relatively long for seeds to be moved at variable distances from their origin and habitat of seed deposition is diverse [25]. The golden lion tamarins use secondary forest, forest edges and forest interior while foraging for fruits. This behavior is responsible for a flow of seeds between habitat types. In this way the golden lion tamarins and other frugivores that disperse seeds contribute to the regeneration of the Atlantic Forest [25].

Decreases in numbers of frugivorous seeds dispersers leads to a loss of recruitment of many plant species in fragmented landscapes [46]. The extinction of the golden lion tamarins from many forest fragments where they originally occurred can be correlated with the impoverishment of these areas in terms of forest regeneration.

The reintroduced population of golden lion tamarins established in the União Reserve through translocation, seems to be contributing, through the dispersal of seeds, to the improvement in the general habitat quality of the area, to the enrichment of degraded areas deep inside the Reserve, and to the regeneration of forest edges. The above considerations also need to take into account the complex interactions among seed dispersers, seeds predators and secondary dispersers which may determine the ultimate fate of seed [47].

Acknowledgements

This study was supported by FAPESP (02/09293-6), Cleveland Metroparks Zoo/Scott Neotropical Fund and CI/Primate Action Fund. We are grateful to the Depto. de Ecologia (IB-USP) and Associação Mico-Leão-Dourado (AMLD) for the institutional support; to the International Committee for the Conservation and Management of Lion Tamarins (ICCM for *Leontopithecus*), and IBAMA for the permission to work in the UBR. We thank Dr. Paulo Nogueira-Neto and Dr. Sérgio Tadeu Meirelles (IB-USP) and the Translocation Team: M.Cecília Kierulff, Sandro V.da Rocha, Susie Pinto, Nailton Azevedo, Hamilton Camargo-Filho, Mateus Carvalho, Walter Silva and all the people who collaborated with this work. We thank two anonymous reviewers for helpful comments on earlier drafts of this paper

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Appendix 1. Percentage of germination of control seeds "C" (from fruits, or with pulp) and of treatment seeds "T"(from feces or spit out) and percentage of seedlings from germinated seeds in the União Biological Reserve, RJ-Brazil. Tamarins' role: (+) (seeds benefited by tamarins); (-) (seeds harmed by tamarins); (=) (similar germination between control and treatment seeds). ns: seed germination or number of seedlings without significant differences; * species with spit seeds; (T): number of tests performed

Species	Nº seeds T / C	Nº seeds germinated T / C	% germination T / C		χ^2	p	Nº seedlings T / C	% seedlings T / C		χ^2	p	Nº seedlings survived
Cecropia hololeuca	seeds< 3mm	1 / 0	seeds< 3mm		-	-	1 / 0	seeds< 3mm		-	-	0
Pourouma guianensis	3 / 0	3 / 0	100	-	-	-(+)	3 / 0	100		-	-	1 / 0
Euphorbiaceae sp.1	9 / 7	3 / 2	33.	28.6	0.22	ns(=)	1 / 2	33.33	100	32.4	<0.001	0 / 0
Inga edulis (T1)	0 / 5	0 / 5	-	100	-	-	0 / 5	-	100	-	-	0 / 2
I. edulis (T2)	0 / 1	0 / 1	-	100	-	-	0 / 1	-	100	-	-	0 / 1
I. edulis (T3)	6 / 6	1 / 4	16.	66.7	28.79	<0.001(-)	1 / 4	100	100	0	ns	1 / 2
I. edulis (T4)	0 / 1	0 / 1	-	100	-	-	0 / 1	-	100	-	-	0
I. edulis (T5)	7 / 7	0 / 1	0	14.3	12.37	<0.01(-)	0 / 1	-	100	-	-	0
I. edulis (T6)	4 / 4	4 / 2	100	50	16.01	<0.001(+	4 / 2	100	100	0	ns	2 / 0
I. edulis (T7)	6 / 6	6 / 5	100	83.33	1.33	ns(=)	2 / 4	33.33	80	18.40	<0.001	1 / 3
I. thibaudiana (T1)	4 / 4	0 / 2	0	50.0	48.02	<0.001(-)	0 / 1	-	50	-	-	0
I. thibaudiana (T2)	5 / 5	0 / 1	0	20	18.05	<0.001(-)	0 / 1	-	100	-	-	0
I. thibaudiana (T3)	6 / 6	4 / 6	66.	100	6.26	<0.05(-)	4 / 6	100	100	0	ns	1 / 2
I. thibaudiana (T4)	1 / 1	1 / 1	100	100	0	ns(=)	1 / 1	100	100	0	ns	1 / 1
I. sp.2 (T1)	2 / 2	0 / 1	0	50	48.02	<0.001(-)	0 / 1	-	100	-	-	0
I. sp.2 (T2)	2 / 0	2 / 0	100	-	-	-	-	-	-	-	-	-
Miconia cinnamomifolia	seeds<3mm	1 / 0	-	-	-	-(+)	1 / 0	-	-	-	-	0
M. latecrenata	seeds<3mm	0 / 3	-	-	-	-(-)	0 / 3	-	-	-	-	0
Ficus cf. *gomelleira*	seeds<3mm	4 / 0	-	-	-	-(+)	4 / 0	100	-	-	-	0 / 0
Calycorectes sp.1*(T1)	0 / 3	0 / 3	-	100	-	-	0 / 3	-	100	-	-	0 / 3
C. sp.1* (T2)	3 / 3	1 / 2	33.	66.7	10.5	<0.001(-)	-	-	-	-	-	-
C. sp.1 (T3)	13 / 13	13 / 8	100	61.5	8.71	<0.01(+)	10 / 7	76.9	87.5	0.56	ns	9 / 5
C. sp.1 (T4)	14 / 15	11 / 12	78.	80	0.001	ns(=)	10 / 9	90.9	75	1.34	ns	8 / 7
*Eugenia robustovenosa**(T1)	6 / 6	1 / 4	16.	66.7	28.79	<0.001(-)	1 / 1	100	25	53.81	<0.001	1 / 0
*E. robustovenosa** (T2)	7 / 6	1 / 0	14.	0	12.4	<0.001(+	-	-	-	-	-	-
*E. robustovenosa** (T3)	5 / 3	3 / 0	60	0	58.02	<0.001(+	-	-	-	-	-	-
E. sp.1*	9 / 10	5 / 5	55.5	50.0	0.19	ns(=)	3 / 4	60	80	2.58	ns	1 / 3
E. sp.4	13 / 19	8 / 13	61.5	68.4	0.27	ns(=)	4 / 8	50	61.5	0.99	ns	3 / 4
Marlierea sp.1	12 / 12	8 / 6	66.7	50	2.11	ns(=)	6 / 4	75	66.7	0.38	ns	1 / 3
Myrcia fallax	2 / 2	1 / 1	50	50	0	ns(=)	1 / 1	100	100	0	ns	1 / 1
Myrtaceae sp.1* (T1)	8 / 10	6 / 2	75	20	30.7	<0.001(+)	6 / 2	100	100	0	ns	6 / 2
M. sp.1* (T2)	7 / 13	1 / 1	14.3	7.7	1.42	ns(=)	1 / 1	100	100	0	ns	1 / 0
M. sp. 11	13 / 14	9 / 7	69.2	50.0	2.78	ns(=)	4 / 2	44.4	28.6	3.00	ns	2 / 1
Randia sp.1 (T1)	1 / 3	1 / 0	100	0	98.01	<0.001(+)	1 / 0	100	-	-	-	0
R. sp.1 (T2)	14 / 14	2 / 11	14.3	78.6	43.13	<0.001(-)	2 / 11	100	100	0	ns	1 / 6
Tocoyena brasiliensis	14 / 8	12 / 5	85.7	62.5	3.33	ns(=)	3 / 2	25	20	0.36	ns	2 / 2
Pouteria bangii (T1)	0 / 1	0 / 1	-	100	-	-	0 / 1	-	100	-	-	0
P. bangii (T2)	1 / 1	1 / 1	100	100	0	ns(=)	0 / 1	0	100	98.01	< 0.001	0
P. bangii (T3)	0 / 6	0 / 5	-	83.3	-	-	0 / 1	-	20	-	-	0
P. bangii (T4)	8 / 1	1 / 1	12.5	100	65.61	<0.001(-)	-	-	-	-	-	-
P. bangii (T5)	1 / 2	1 / 2	100	100	0	ns(=)	1 / 2	100	100	0	ns	0
P. bangii (T6)	4 / 4	0 / 2	0	50	48.02	<0.001(-)	0 / 2	-	100	-	-	0 / 1
Sarcaulus brasiliensis (T1)	7 / 7	0 / 2	0	28.57	26.6	<0.001(-)	0 / 1	-	50	-	-	0
S. brasiliensis (T2)	0 / 2	0 / 1	-	50	-	-	0 / 1	-	100	-	-	0
S. brasiliensis (T3)	3 / 2	1 / 2	33.33	100	32.34	<0.001(-)	1 / 1	100	50	16.01	< 0.01	0
S. brasiliensis (T4)	6 / 6	1 / 4	16.7	66.7	28.79	<0.001(-)	1 / 4	100	100	0	ns	0
S. brasiliensis (T5)	7 / 9	3 / 9	42.9	100	22.02	<0.001(-)	0 / 4	0	44.4	42.42	<0.001	0 / 2
S. brasiliensis (T6)	22 / 22	15 / 10	68.2	45.4	4.18	<0.05(+)	14 / 9	93.3	90	0.03	ns	9 / 3
Unknown 18	1 / 2	1 / 2	100	100	0	ns(=)	1 / 2	100	100	0	ns	0
TOTAL	**256 / 274**	**137 / 157**	**53.5**	**57.3**	**0.07**	**ns**(=)	**92 / 117**	**71.3**	**76**	**0.09**	**ns**	**52 / 54**