$See \ discussions, stats, and \ author \ profiles \ for \ this \ publication \ at: \ https://www.researchgate.net/publication/230126486$

Frugivory patterns and seed dispersal by golden-headed lion tamarins (Leontopithecus chrysomelas) in Una...

Article *in* Mammalia · November 2011

DOI: 10.1515/MAMM.2011.042

CITATIONS

3

READS

151

4 authors:



Nayara Alcantara Cardoso

7 PUBLICATIONS 30 CITATIONS

SEE PROFILE



Yvonnick Le Pendu

Universidade Estadual de Santa Cruz

45 PUBLICATIONS 346 CITATIONS

SEE PROFILE



Marina J. Lapenta

University of São Paulo

14 PUBLICATIONS 53 CITATIONS

SEE PROFILE



Becky Raboy

University of Toronto

29 PUBLICATIONS 355 CITATIONS

SEE PROFILE

Frugivory patterns and seed dispersal by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Una Biological Reserve, Bahia, Brazil

Nayara A. Cardoso^{1,*}, Yvonnick Le Pendu¹, Marina J. Lapenta² and Becky E. Raboy³

- ¹ Department of Biology, Universidade Estadual de Santa Cruz, Rodovia Ilhéus/Itabuna, km 16 Salobrinho, Ilhéus, Bahia 45662-900, Brazil,
- e-mail: nayara_cardoso@yahoo.com.br
- ² Instituto Pri-Matas para a Conservção da Biodiversidade, Caixa Postal 3304, Savassi, Belo Horizonte, MG. CEP: 30140-970, Brazil
- ³ Smithsonian Conservation Biology Institute, National Zoological Park, 3001 Connecticut Ave NW, Washington DC 20008, USA

Abstract

This study identified fruit species eaten by Leontopithecus chrysomelas (golden-headed lion tamarins; GHLTs) and related their consumption to seed dispersal. Two GHLT groups were monitored from September 2006 through August 2007 in Una Biological Reserve, Bahia, Brazil. GHLTs consumed fruit from 71 species, preferred mature fruit and swallowed the seeds of most species (76.8%). Smaller seeds were swallowed and larger seeds were generally discarded. GHLTs defecated in low quantities and more than 50% of the faeces contained seeds from only one species. Most faeces were deposited far from the parental tree (>20m) and only 24.2% under the parental tree. The defecation pattern of L. chrysomelas could reduce competition between seeds and facilitate the establishment of seedlings from the most consumed species. Faeces were deposited widely throughout home ranges and away from a seed's parental tree increasing the chances that seeds reach favourable environments and avoid competition with other seedlings. Additionally, defecations also occurred in the same habitat type as a seed's parental tree, keeping species within their typical habitat. GHLTs in Una Biological Reserve were efficient dispersers and might play an important role in the maintenance of floristic composition and regeneration of habitat.

Keywords: Atlantic forest; frugivory; *Leontopithecus chrysomelas*; primates; seed dispersal; South America.

Introduction

Seed dispersal by animals (zoochory) is the most common method of seed dispersal in tropical forests (Janzen 1980).

Zoochory is important for maintaining populations of various species of plants and conserving heterogeneity of the floristic composition (Howe 1984, Garber and Lambert 1998). However, the efficacy of animals as seed dispersers depends on their ability to manipulate fruit and on their patterns of seed displacement, among other factors (Van Der Pijl 1982).

Most primates consume fruit, although the wide variation in primate morphology, physiology and feeding behaviour leads to different treatment and defecation patterns of fruits and seeds. These differences in turn, influence the quality of primates as seed dispersers (Poulsen et al. 2001, Wehncke et al. 2004, Mcconkey 2005). Those that swallow and defecate or spit a great quantity of seeds in places that promote the seed's survival and growth are known to be important dispersers (Chapman and Onderdonk 1998). Several studies have documented seed dispersal by primates in tropical forests (Coates-Estrada and Estrada 1988, Passos 1997, Yumoto et al. 1999, Oliveira and Ferrari 2000, Stevenson 2000, Knogge et al. 2003, Bravo 2009, Vanderhoff and Grafton 2009). However, information related to the quality of the deposition sites for germination and survival of the seeds is still scarce for most species.

Lion tamarins (*Leontopithecus* sp.) are primate frugivores that consume fruit from a variety of plant species (Passos 1997, Kierulff et al. 2002, Lapenta et al. 2003, Raboy and Dietz 2004, Catenacci et al. 2009). Fruit makes up most of the lion tamarins' diet and they spend up to 12% of their day searching for and eating fruit (Raboy and Dietz 2004). They generally prefer small, ripe, soft and sweet fruits (Kierulff et al. 2002), although large ones are also consumed occasionally (Lapenta et al. 2003). Studies by Passos (1997), Lapenta and Procópio-de-Oliveira (2008, 2009), Lapenta et al. (2008) and Catenacci et al. (2009) indicate that lion tamarins act as legitimate dispersers for some plant species.

Leontopithecus chrysomelas is listed as "Endangered" according to the IUCN Red List (Kierulff et al. 2008) due to the destruction and alteration of its natural habitat. Golden-headed lion tamarin populations suffered a significant reduction and loss of habitat in recent decades (Rylands et al. 2002, Raboy et al. 2010). Although patterns of seed dispersal have been studied in GHLTs living in degraded and heterogeneous habitats (Catenacci et al. 2009), seed dispersal by GHLTs living in more homogeneous and less disturbed habitats has yet to be reported. The aim of this study therefore was to identify the fruit species consumed by L. chrysomelas in a relatively undisturbed portion of Una Biological Reserve, Bahia, Brazil, and relate this consumption with the dispersion of seeds. This information contributes to our understanding of zoochory within the Atlantic forest and has

^{*}Corresponding author

great utility towards elaborating conservation measures for GHLTs and their forests.

Materials and methods

Study area

This study was conducted in the eastern portion of the Una Biological Reserve (15° 10′S, 39° 03′ W), Brazil. The current area of the reserve is 18,500 ha (ICMBIO 2010). According to Köppen, the regional climate is classified as Af/tropical forest climate, hot humid and with no defined seasonality (Gouvêa et al. 1976). The average annual temperature of the region is 24°C and the precipitation is approximately 2000 mm/year. The eastern portion of the reserve and its surroundings are represented mostly by mature forests, although it also has some regenerating forests in different stages of succession, cabruca forest and swamps. Cabruca is an agroforestry system in which cocoa trees are planted under the forest canopy for shade. Some trees have been selectively removed in this habitat.

Study groups

Two groups of GHLTs (ONC and TAP) were tracked monthly by radio telemetry (from September 2006 to August 2007, with the exception of November 2006). Two adult individuals of each group were previously fitted with radio collars to facilitate location and identification of the group as part of a long term GHLT monitoring program. During the study period, ONC group size varied between six and eight individuals, and TAP between six and seven individuals. Groups were monitored for 2 to 3 days each month, from the moment they emerged from their sleeping site until the end of the day, when they returned to their overnight site. A total of 377 h of monitoring were conducted during 35 complete days (ONC, 148.5 h in 15 days; TAP, 228.5 h in 20 days).

Data collection

The start and end times of feeding activities were recorded. A feeding bout was defined as the time when the first individual in the group began eating the fruit at a specific tree until the time the last individual to eat consecutively in that tree stopped eating. For each feeding tree, the following data were recorded: geographic location of the tree, state of maturation of the consumed fruit (immature, mature or both), colour of the consumed fruit, processing method of the seed (swallowed, spat out, discarded or preyed on) and habitat type where they were found (mature, secondary, cabruca or swamp). Whenever possible, samples of the consumed fruit were collected for morphological characterization (colour, length and diameter of the fruits and seeds). The seed processing categories were assigned according to observations of seed consumption and visual analysis of the faeces. We considered the processing category most frequently recorded for each species. "Swallowed" was scored when the seeds passed through the digestive tract and were encountered in the faeces. "Spat out" was scored when seeds were put in the mouth and later spat out, and only the pulp was consumed. "Discarded" was scored when the seeds were not put in the mouth and only the pulp was consumed. "Preyed on" was scored when the seeds were damaged or bitten together with the pulp and/or pieces were found in the faeces.

The habitat types were defined according to Raboy and Dietz (2004): mature forest was characterized by a canopy at 25-35 m height, abundant epiphytes and vines, and a relatively open understory. Cabruca had a similar height and presence of epiphytes but also had cacao and banana trees, a sparser mid-story, and no vines. Secondary forests had canopies at 5-15 m with trees of small diameter and dense, scrubby understory. Secondary forests also included small areas of newly regenerating fields with few trees and mainly bushes and grasses. Swamps (located within mature or secondary forests) were classified as a distinct habitat type, characterized by muddy ground or standing water and had the densest understory.

Faeces were collected opportunistically during the monitoring of the animals and the following information was recorded for each deposition: geographic location of the faeces, time of deposition and habitat type where the faeces were deposited. The geographic location of the feeding trees and faeces were estimated using a map of the study area and marked trails (Raboy et al. 2004).

Data analyses

The information from the two groups, which used a large portion of overlapping area and the same habitat types, was aggregated to increase sample size.

In order to verify if seed processing was influenced by the seed's size (length and diameter), we conducted an ANOVA and Tukey's mean comparison test. Seeds estimated to be smaller than 3 mm (n=11 species) were excluded from this analysis following Lapenta et al. (2003) and Lapenta and Procópio-de-Oliveira (2008) but were included in other analyses.

In order to calculate the percentage of each habitat in a group's home range, the size and location of each home range was determined by plotting the respective groups feeding tree locations in ArcGIS 9.3 and calculating the Minimum Convex Polygon. These home ranges were then overlaid on a vegetation map of the study site (Raboy et al. unpublished data) that included mature, secondary, swamp, cabruca, open field, and rubber tree plantations.

To determine the dispersal distance of the seeds, the Euclidean distance was calculated from the parental tree to the point of deposition. When the feeding trees of the same species were consumed in sequence, the data were discarded because it was not possible to identify the correct parent tree for the seeds found in faeces. Similarly, when faeces were deposited first thing in the morning and the parental tree of the seeds was unknown, distances could not be calculated.

We analyzed the flow of seeds between different habitat types for the most consumed species by comparing of the habitat type of the parental tree and of the site of faeces deposition.

Table 1 Most common plant species in the diet of the GHLTs.

Species	Feeding trees	Feeding bouts		
Henriettea succosa	20 (8.9%)	21 (8.6%)		
Cheiloclinium cognatum	15 (6.7%)	16 (6.5%)		
Manilkara maxima	13 (5.3%)	16 (6.5%)		
Pourouma acutiflora	14 (6.2%)	14 (5.7%)		
Passifloraceae sp.	12 (5.3%)	14 (5.7%)		
Myrcia fallax	11 (4.9%)	14 (5.7%)		
Inga subnuda	8 (3.6%)	10 (4.1%)		
Other	132 (58.6%)	140 (57.1%)		

The values indicate the number of trees used for consumption of fruits and number of visits for each species.

Results

Plant species consumed

Individuals of both groups consumed fruits of 71 plant species. Of those, 58 were identified and distributed in 23 families (Appendix 1). Seven species were most consumed, particularly Henrietea succosa, Cheiloclinium cognatum, Manilkara maxima, and Pourouma acutiflora (Table 1). In contrast, 45% (n=32) of the species were only consumed

GHLTs swallowed seeds of 53 species (76.8%), spat 11 out (15.9%) and only discarded two: Elaeis guineensis and Cathedra sp. The number of species that had their seeds preyed on was low (n=3) and we did not observe damaged seeds in the faeces.

Morphological characteristics of the fruits

The fruits of 89.8% of the species were consumed mature, 5.8% were either mature or immature and 4.3% were immature. Species of yellow fruits represented most of the consumption (27.5%), followed by green (18.8%) and black or purple (14.9% each). The size of the fruits (n=35 species)consumed by the lion tamarins showed great variation. Mean length differed between 7.4 and 198.3 mm per species and mean diameter between 5.7 and 39.1 mm. The size of the seeds (n=42 species) also showed large variation. Mean length was 15.7 ± 6.7 mm and mean diameter 9.0 ± 4.0 mm. Seeds that were spat out and discarded showed greater length and diameter than ones that were swallowed or preyed on (Table 2). The seed processing varied significantly according to its length $(F_{3,191}=109.09, p<0.0001)$ as well as diameter $(F_{3, 191}=64.37, p<0.0001)$ and all mean comparison tests between treatments were significant (p<0.005).

Table 2 Average seed sizes (±standard deviation) according to the seed processing method.

Processing method	Mean length (mm)	Mean diameter (mm)
Discarded (n=8)	29.59±4.9	16.84±1.7
Spat out (n=36)	21.73 ± 5.75	13.43 ± 4.35
Swallowed (n=147)	11.20 ± 3.59	7.68 ± 2.43
Preyed on (n=4)	5.85 ± 0.37	3.73 ± 0.32

Defecation pattern and dispersion distance

Of the 282 defecations found (average of seven samples/ day), 227 (80.4%) contained seeds. Only 40 (75.4%) of the 53 species that had their seeds swallowed by lion tamarins during our study were found in these faeces. The maximum number of different species found in the faeces was three and in 155 (54.9%) depositions, there were seeds of a single species. Apart from a few seeds, the faeces found were composed of little faecal material.

The lion tamarins moved the swallowed seeds distances between 22 to 781 m away from the parental tree (n=120 depositions), with most depositions at over 150 m (61%, n=74) (Figure 1). However, 29 (24.2%) faeces were deposited under the canopy of the source tree (not considering the seeds that were spat out or discarded).

The seeds were dispersed across the groups' home ranges (Figure 2) in different habitat types. A greater number of depositions (84.3%) were found in areas of mature and secondary forests, and in lower quantities in swamp and cabruca (11.8%). The proportion of depositions in each habitat type was similar to the proportion of numbers of trees used for fruit consumption in the different habitat types. Fruit consumption, as well as deposition, were more frequent in areas of mature and secondary forests (Figure 3). The amount of secondary and mature forests was greater than other habitats for both groups (Table 3).

For the most consumed species, the flow of seeds was greater to the same habitat type where conspecific trees, used in fruit consumption, were present (Table 4). However, the seeds were also transported to habitats other than the site of consumption, although in smaller proportions.

Discussion and conclusion

Plant species consumed

Leontopithecus spp. exploit a large number of plant species for fruit consumption. However, the number of species exploited vary between the different species of tamarins according to the area and duration of the study (Raboy 2002, Procópio-de-Oliveira et al. 2008). In particular, GHLTs in Una Biological Reserve consume some of the greatest diversity of plant species (79 spp. for Raboy et al. 2004, 92 spp. for Catenacci 2008, 93 spp. for Oliveira et al. 2010). Several studies of other Leontopithecus species (of similar length) report plant species diversities between 30 and 97, with most less than 60 species (as reviewed in Kierulff et al. 2002 and from Lapenta and Procópio-de-Oliveira 2008). The diversity of fruits species consumed by GHLTs could be explained by the high plant diversity and richness in the Una region (Mariano-Neto 2004, Raboy et al. 2004, Amorim et al. 2008) and also by the wide variety of vegetation used by the studied groups (cabruca, swamp, mature, secondary). Although a great diversity of species was consumed by our study GHLTs, we also noted a more intense utilization of a smaller subset of species, a common feeding characteristic of Leontopithecus (Kierulff et al. 2002).

Figure 1 Frequency distribution of seeds dispersed to each distance class.

Mature and secondary forests possess structural differences as well as differences in plant species composition and degrees of disturbance (Tabarelli and Mantovani 1999, Suscke 2009). These differences lead to variation in the abundance and productivity of resources present in these forests. In mature forest, resource availability is generally lower than in secondary forest, but species diversity is greater (Mariano-Neto 2004, Pessoa 2008). The higher reproductive activity and a higher number of pioneer species in secondary forest lead to greater resource availability for frugivores (Pessoa 2008). Although Manilkara maxima is common in mature forest and Henriettea succosa a pioneer species of secondary forest and clearings, both species present the same reproductive strategy at our study site, producing flowers and fruits most of the year, with 1-3 months intervals without resources (Suscke 2009, Pessoa et al. 2011).

The patterns of spatial distribution and fruit availability of both *Manilkara maxima* and *Henriettea succosa* and their high rates of consumption in this study indicate their importance as potential food resources for GHLTs in Una Biological Reserve. Correspondingly, Oliveira et al. (2010) ranked these two species as "Extremely Valuable", the highest category possible in an index of key tree species used by GHLTs based on a plant species versatility of function as a GHLT resource, their attractiveness, prevalence across multiple habitats and frequency of use patterns. These species were also important in the diet of *Cebus xantosthernos* ranging in the same area during our study (Suscke, 2009). Due to their importance for GHLTs and other primates (Raboy et al. 2008, Suscke 2009), these plant species should be taken into consideration in conservation measures, whether it is for resto-

ration of degraded areas or for the maintenance of the forests they occupy.

Morphological characteristics of the fruits

Lion tamarins consume more ripe than unripe fruit in their diet (Rylands 1989, Kierulff et al. 2002, Lapenta et al. 2003) and swallow most seeds, similar to other Callitrichidae: Saguinus mystax and Saguinus fuscicollis (Oliveira and Ferrari 2000, Knogge and Heymann 2003), Callithrix jacchus (Castro et al. 2003) and other primates such as Cebus capucinus (Wehncke et al. 2003) and Alouatta palliata (Souza 1999). In general, callitrichids are primates of small body size and the morphology of their digestive tract does not allow large seeds to be swallowed. As observed by Lapenta et al. (2003) for Leontopithecus rosalia, GHLTs from the Una Biological Reserve consumed fruits with seeds of various sizes, although usually the smaller seeds were swallowed and larger ones were discarded. Castro et al. (2003) also found the same result for Callithrix jacchus and Saguinus niger. However, Lapenta et al. (2003) verified that this swallowing behaviour was more related to the elongated shape of the seeds and the adherence of the pulp than to their size.

The colour of the fruit, nutritional quality of the pulp, degree of protection and size of the seed have all been suggested as fruit characteristics defining their attractiveness for the primary dispersing agent (Janson 1983). Colour vision is important in the discrimination of fruits and for many primates the level of maturation of the fruits is obtained through its colour, together with its morphology (e.g., size and weight) and orient fruit choice (Urbani 2002). Terborgh

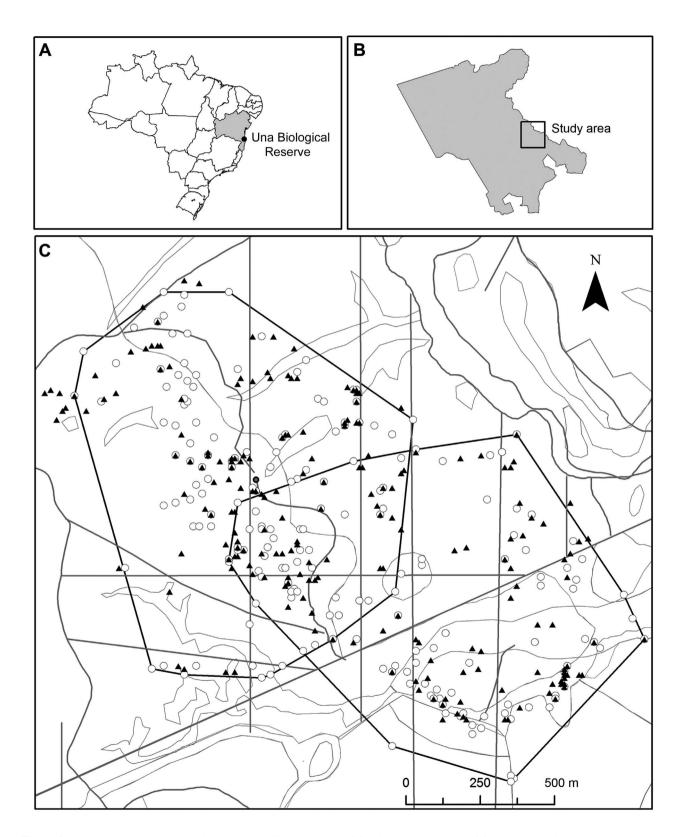


Figure 2 (A) Brazil. (B) Una Biological Reserve. (C) Distribution of fruiting trees used and of faeces deposited by GHLT. The circles correspond to the fruiting trees and the triangles to the faeces deposited. The groups' home ranges are based on the location of the fruiting trees used during the study period.

Figure 3 The distribution of defecations and fruiting trees used by GHLTs in different habitats.

(1983) and Gautier-Hion et al. (1985) reported a preference for fruits of yellow, orange and red colours for primates of Peru and Africa, respectively, suggesting that yellow and orange fruits contrast with the green foliage of the plants, enhancing visibility of these colours. Golden lion tamarins (Procópio-de-Oliveira 2002, Lapenta et al. 2003) and the GHLTs in this study consumed yellow, black, purple and green fruits in greater quantities and less red, similar to *Saguinus* (Smith et al. 2003). Callitrichids have a polymorphic system of colour vision as is true for most Neotropical primates, whereby individuals may be di- or trichromatic (Smith et al. 2003). Dichromats, which include all males and some females, have difficulty in distinguishing red and green. This may explain the low numbers of red fruits consumed by our study groups, in particular if red is not easily

Table 3 The proportion of habitat types in the GHLTs home ranges.

Group	Mature (%)	Secundary (%)	Swamp (%)	Cabruca (%)	
ONC	59.9	37.9	5.2	_	
TAP	32.7	48.8	10.9	7.6	

Mat, mature; Sec, secondary; Swa, swamp; Cab, cabruca.

distinguished from the predominantly green background of the forest. Dichromatic vision is believed to help in breaking up colour-camouflaged fruit (Stoner et al. 2005) especially in certain lighting (Caine et al. 2010) and this could explain why green and yellow (which would be perceived as greener by dichromats), as well as other darker and duller forest colours like black and purple were favoured by lion tamarins. Alternatively, GHLTs as well as other primates could be eating coloured fruit in relation to their availability in the forest. Further studies including experimental manipulation of food choice in the field and phenological sampling can help elucidate colour choice in GHLTs.

Defecation pattern and dispersion distance

Primates can be involved in the germination process by disseminating seeds and/or influencing the percent or rates of germination (Wrangham et al. 1994, Serio-Silva and Rico-Gray 2002, Castro et al. 2003, Martins 2006). The effect of primates on the germination process can be beneficial, neutral or even detrimental. Although lion tamarins are considered legitimate dispersers due to germination viability of ingested seeds (Lapenta et al. 2008; Catenacci et al. 2009), they have not been shown to alter percent or rates of germination significantly over control seedlings that were not ingested. Despite their potential neutrality to seedling germination, the tamarins do play an important role in other aspects of seed dispersal such as dispersal distance and placement of seed deposition (Lapenta and Procópio-de-Oliveira 2008).

Some authors suggest that the best advantage offered by dispersers to plants is the distribution of seeds in favourable habitats or sites where their chances of survival are increased (Wrangham et al. 1994, Garber and Lambert 1998, Andresen 1999). The extent of this advantage depends mainly on the defecation pattern of the disperser. Primates show various defecation patterns that can affect seed survival (Knogge et al. 2003, Wehncke et al. 2004, Lapenta and Procópio-de-Oliveira 2009). Janzen (1980) showed that defecations in small piles containing many seeds deposited randomly are better than large defecations in specific sites (as latrines in *Alouatta*). The depositions in large aggregations decrease the efficacy of disperser because these clumps attract more pred-

Table 4 Habitat types of fruiting trees and defecation of the species most consumed by GHLTs.

Species	Feeding tree				Depositions			
	Mat	Sec	Swa	Cab	Mat	Sec	Swa	Cab
Henriettea succosa		18	2		5	23		3
Cheiloclinium cognatum	15				11	2		
Pourouma acutiflora	7	7				4		
Passifloraceae sp.	6	6			15	12		
Myrcia fallax		11			1	12		
Inga subnuda		6		2		3	1	2

The values represent the number of defecations with seeds of species and fruiting trees used in their respective habitats. *Manilkara maxima* was not included because the seeds of this species were spat out.

ators and impose higher intraspecific competition for the seeds.

GHLTs in this study defecated a limited number of species in small quantities per defecation, so that more than 50% of the faeces contained seeds of only one species. Furthermore, little faecal material was found in these faeces. Seeds deposited with larger quantities of faecal material increase the attractiveness for seed predators and have greater probability of removal than the ones deposited with small quantities or no faecal material (Zhang and Wang 1995, Wehncke et al. 2004). This deposition pattern was also found in Leontopithecus rosalia (Lapenta and Procópio-de-Oliveira 2008) and in Leontopithecus chrysomelas (Catenacci et al. 2009), Saguinus mystax and Saguinus fuscicollis (Knogge and Heymann 2003) and allows less intra- and inter-specific competition between seeds and consequently between the growing seedlings (Knogge and Heymann 2003). In addition to differences in deposition patterns, differences in behavioural and feeding patterns of primate species result in differences in their efficacy as dispersing agents (Andresen 1999, Martins 2006). When compared with other Neotropical primates, lion tamarins use large home ranges and travel long daily distances in relation to their body size (Dietz et al. 1997). The average daily distance covered by three GHLT groups in Una Biological Reserve was ca. 1750 m (Raboy and Dietz 2004), allowing the animals to travel long distances and across different types of vegetation during the day. GHLTs deposited faeces more frequently between 50 and 200 m away from the parental tree, so that there is less competition for resources, less attraction of predators (Lapenta and Procópio-de-Oliveira 2008) and an increase in the probability of seed survival following the escape hypothesis (Janzen 1970). In addition to dispersing seeds away from the parental trees, GHLTs deposited faeces across their whole home range, taking seeds to different habitat types, including small areas of newly regenerating fields with few trees and mainly bushes and grasses. This allows some species to colonize sites free from competition (Howe and Smallwood 1982). The same results were found by Catenacci et al. (2009) for GHLTs in a very degraded and heterogeneous habitat.

The home ranges of both study groups consisted of mainly mature and secondary forests, although the use of such areas could be unrelated to their availability in the groups' home ranges. Raboy and Dietz (2004) suggested that the preferential use of certain types of vegetation by GHLTs could be related to the variation in the quality and density of resources. Mature and secondary forests of Una Biological Reserve presented greater density of trees (Raboy et al. 2004, Oliveira et al. 2010) and species diversity (Pessoa 2008) than cabruca and swamp. Therefore, they might offer higher density food resources for GHLTs and explain why they were more commonly visited for fruit in this study.

The type of vegetation where seeds are deposited plays an essential role in the survival or growth of seedlings. Furthermore, microclimatic factors (humidity, light and temperature) vary in conserved areas and disturbed tropical forests, influencing significantly the germination of seeds (Serio-Silva and Rico-Gray 2002). When considering the most representative plant species in the GHLT diet, most seeds were deposited in the habitats in which the fruit trees eaten by GHLTs were more frequently found. Catenacci et al. (2009) reported the same results for most plant species dispersed by GHLTs in the western portion of the reserve. This defecation pattern contributes to the maintenance of specific plant diversity unique within each habitat. However, GHLTs also dispersed seeds across different types of vegetation, especially in secondary forests. According to Galleti et al. (2004), restoration of degraded habitats can be accelerated by the aid of seed dispersing animals, given that they take seeds from primary forests to disturbed areas. Some studies of Callitrichidae show that these primates are important seed dispersing agents in forests where they dwell and contribute to ecological succession in secondary forests (Knogge et al. 1998, Oliveira and Ferrari 2000, Castro et al. 2003, Knogge et al. 2003, Lapenta et al. 2008).

Studies suggest that the loss of primates in some tropical forests can have negative consequences for the recruitment of plant species included in the diets of those primates (Chapman and Onderdonk 1998, Link and Fiore 2006). Understanding how the plant-animal interactions occur is fundamental towards understanding the ecosystem and can help in the development of conservation measures, especially, for the management of areas where the species occur. The GHLT frugivory and defecation patterns presented in this study were similar to those recorded for the genus and for other Callitrichidae, supporting the role of this group of primates as potential seed dispersers in areas they occupy. The region of Una Biological Reserve represents a major block of the remaining southern Bahia forest and conservation measures are being undertaken to maintain its forests, such as strengthening of an ecological corridor within the region (MMA 2011). Plant species listed in this study could be used in the development of this corridor and in this way GHLTs can facilitate the natural regeneration dynamics in forest habitats. In summary, our results indicate that GHLTs might have an important role in maintaining within-habitat floristic diversity as well as contributing to the regeneration of degraded areas in Una Biological Reserve and maybe for the Atlantic forest biome in Southern Bahia.

Acknowledgements

Field work was carried out within the infrastructure of the Golden-Headed Lion Tamarin Project (PIs B.E. Raboy and J.M. Dietz). We thank the Instituto de Estudos Socioambientais do Sul da Bahia (IESB) and Universidade Estadual de Santa Cruz (UESC)-Zoology Postgraduate Program for providing institutional and logistic support. We thank IBAMA for the permission to work in Una Biological Reserve (Licence number 12279-1) and FAPESB for the scholarship grant to N.A. Cardoso (Term 1629/2006). We are extremely grateful to Gilvan Gomes Mota and Jiomário dos Santos Souza for their field assistance and to James Dietz, Lilian Catenacci, Kristel De Vleeschouwer, Leonardo Neves and Carlos Guidorizzi for their assistance with GHLT captures and/or processing during the study period.

Appendix

Appendix 1 List of plant species, number of fruiting tree used, seed processing, ripeness and colour of fruits consumed by GHLT in the study.

Family	Species	Number of tree#	Processing of the seed	State of maturation	Colour
Anacardiaceae	*Tapirira guianensis	3 (3)	Swallowed	Mature	Black
Annonaceae	*Rollinia bahiensis	4 (4)	Swallowed	Mature	Yellow
Apocynaceae	*Lacmellea bahiensis	3 (3)	Swallowed	Mature	Yellow
	*Macoubea guianensis	6 (7)	Swallowed	Mature	Green
Araceae	*Philodendron bipinnatifidum	6 (8)	Swallowed	Mat/immature	Green
	*Araceae sp. 1	4 (5)	Swallowed	Mature	Green
	*Araceae sp. 2	2 (2)	Swallowed	Mature	Green
Arecaceae	Elaeis guineensis	6 (6)	Discarded	Mature	Orange
	*Bactris setosa	1 (1)	Swallowed	Mature	Purple
Boraginaceae	*Cordia sp.	1 (1)	Swallowed	Mature	Yellow
Bromeliaceae	*Aechmea sp.	3 (3)	Swallowed	Mature	Brown
	Lymania azurea	2 (2)	Preyed on	Immature	Green
	*Bromeliaceae sp. 1	1 (1)	Swallowed	Mature	Brown
	*Bromeliaceae sp. 2	1 (1)	Swallowed	Mature	Brown
	Bromeliaceae sp. 4	1 (1)	Preyed on	Immature	Green
Burseraceae	Tetragastris catuaba	2 (2)	Spat out	Mature	Yellow
Clusiaceae	Symphonia globulifera	2 (2)	Spat out	Mature	Brown
Ebenaceae	Dyospiros sp.	1 (1)	Swallowed	Mature	Brown
Salicaceae	*Casearia bahiensis	3 (4)	Swallowed	Mature	Yellow
Malpighiaceae	*Byrsonima sp.	1 (1)	Swallowed	Mature	Green
Melastomataceae	*Henriettea succosa	20 (21)	Swallowed	Mature	Purple
	*Miconia mirabilis	4 (4)	Swallowed	Mature	Purple
Mimosaceae	*Inga tenuis	1 (1)	Swallowed	Mature	Brown
Mimosaceae	*Inga subnuda	8 (10)	Swallowed	Mature	Brown
Moraceae	*Ficus hirsuta	2 (2)	Swallowed	Mature	Green
	*Ficus sp. A	1 (1)	Swallowed	Mature	Red
	*Ficus sp. C	1 (1)	Swallowed	Mature	Red
	*Ficus sp. B	1 (1)	Swallowed	Mature	Green
	Helicostyles tomentosa	3 (4)	Swallowed	Mature	Yellow
	*Pourouma acutiflora	14 (14)	Swallowed	Mature	Purple
	*Pourouma guianensis	3 (3)	Swallowed	Mature	Purple
Myrtaceae	Eugenia itapemirimensis	1 (1)	Spat out	Mature	Black
мупасеае	*Myrcia fallax	11 (14)	Swallowed	Mature	Black
	*Myrtacea sp. 1	1 (1)	Swallowed	Mature	Black
	Myrtacea sp. 2	2 (2)	Swallowed	Mature	Black
	Myrtacea sp. 3	1 (1)	Swallowed	Mature	Black
	Myrtacea sp. 4	1 (1)	Swallowed	Mature	Red
	Myrtacea sp. 5	1 (1)	Swallowed	Mature	Black
	Myrtacea sp. 6	1 (1)	Swallowed	Mature	Purple
	Myrtacea sp. 7	2 (2)	Swallowed	Mature	Black
Olacaceae	Cathedra sp.	1 (1)	Discarded	Mature	Yellow
Passifloraceae	*Passiflora quadrangularis	1 (1)	Swallowed	Mature	Yellow
ussilioi us suc	*Passifloraceae sp. 1	12 (14)	Swallowed	Mature	Yellow
Rubiaceae	*Randia armata	4 (4)	Swallowed	Mature	Yellow
	*Tocoyena bullata	1 (1)	Swallowed	Mat/immature	Green
Sapindaceae	Talisia cerasina	3 (3)	Spat out	Mature	Yellow
Sapotaceae	Chrysophyllum splendens	4 (4)	Spat out	Mature	Red
Japonicono	Diploon cuspidatum	4 (4)	Spat out	Mat/immature	Yellow
	Ecclinusa ramiflora	1 (1)	Spat out	Mature	Yellow
	Manilkara cf. salzmanii	1 (1)	Swallowed	Mature	Orange
	тиниката сј. запуншни	1 (1)	5 wano wea	14141410	Orange
	Manilkara maxima	13 (16)	Spat out	Mature	Brown

(Appendix 1 continued)

Family	Species	Number of tree#	Processing of the seed	State of maturation	Colour
Sapotaceae	*Micropholis guianensis	3 (3)	Swallowed	Mature	Brown
	Sapotaceae sp. 1	3 (3)	Swallowed	Mature	Green
	Sapotaceae sp. 2	1 (1)	Spat out	Mature	Purple
Violaceae	Rinorea guianensis	1 (1)	Swallowed	Mature	Purple
Hypocrateaceae	*Cheiloclinium cognatum	15 (16)	Swallowed	Mat/immature	Yellow
	Unknown 1*	2 (2)	Swallowed	Mature	Yellow
	Unknown 2*	6 (7)	Swallowed	Mature	Black
	Unknown 3*	1 (1)	Swallowed	Mature	Black
	Unknown 4	2 (2)	Swallowed	Mature	Yellow
	Unknown 5*	1 (1)	Swallowed	Mature	Purple
	Unknown 6	1 (1)	Spat out	Mature	Green
	Unknown 7*	1 (1)	Swallowed	Mature	Green
	Unknown 8	1 (1)	Preyed on	Mature	Purple
	Unknown 9	1 (1)	Swallowed	Mature	Yellow
	Unknown 10	1 (1)	Swallowed	Mature	Red
	Unknown 11*	1 (1)	Swallowed	Mature	Yellow
	Unknown 12	1 (1)	Swallowed	Mature	Purple
	Unknown 13	1 (1)	Spat out	Mature	Yellow

^{*}Values in parentheses represent the number of visits for each species.

References

- Amorim, A.M., W.W. Thomas, A.M.V. Carvalho and J.G. Jardim. 2008. Floristic of the Una Biological Reserve, Bahia, Brazil. In: (W.W. Thomas, ed.) The Atlantic coastal forests of northeastern Brazil. New York: Memoriam of New York Botanic Garden, NY. pp. 67-146.
- Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. Biotropica 31: 145-
- Bravo, S.P. 2009. Implications of behavior and gut passage for seed dispersal quality: the case of black and gold howler monkeys. Biotropica 41: 751-758.
- Caine, N.G., D. Osório and N.I. Mundy. 2010. A foraging advantage for dichromatic marmosets (Callithrix geoffroyi) at low light intensity. Biology Letters 6: 36-38.
- Castro, C.S.S., A.A.B. Marques, P. Izar, A.C.M. Oliveira and M.A. Lopes. 2003. The role of primates as seed dispersers in the vegetation structure of tropical forests. Neotropical Primates 11:
- Catenacci, L.S. 2008. Ecologia alimentar do mico-leão-da-caradourada Leontopithecus chrysomelas (Kuhl. 1820) (Primates: Callitrichidae) em áreas degradadas da Mata Atlântica do sul da Bahia Msc Dissertation. Universidade Estadual de Santa Cruz, Bahia. pp. 139.
- Catenacci, L.S., K.M. De Vleeschouwer and S.L.G. Nogueira-Filho. 2009. Seed dispersal by golden-headed lion tamarins Leontopithecus chrysomelas in Southern Bahia Atlantic forest. Brazil. Biotropica 41: 744-750.
- Chapman, C.A. and D.A. Onderdonk. 1998. Forests without primates: primate/plant codependency. Am. J. Primatol. 45:
- Coates-Estrada, R. and A. Estrada. 1988. Frugivory and seed dispersal in Cymbopetalum baillonii (Annonaceae) at los Texas, México. J. Trop. Ecol. 4: 157-172.
- Dietz, J., C.A. Peres and L. Pinder. 1997. Foraging ecology and use

- of space in wild golden lion tamarins (Leontopithecus rosalia). Am. J. Primatol. 41: 289-305.
- Galleti, M., M.A. Pizo and P.C. Morellato. 2004. Fenologia, frugivoria e dispersão de sementes. In: (L. Cullen Jr., R. Rudran, C. Valladares-Pádua, ed.) Métodos de estudos em biologia da conservação e manejo da vida silvestre. Editora da Universidade Federal do Paraná, Curitiba, PR. pp. 395-422.
- Garber, P.A. and J.E. Lambert. 1998. Introduction to primate seed dispersal. Primate as seed dispersers: ecological processes and directions for future research. Am. J. Primatol. 45: 3-8.
- Gautier-Hion, A., J.-M. Duplantier, R. Quris, F. Feer, C. Sourd, J.-P. Decoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, A. Moungazi, C. Roussilhon and J.-M. Thiollay. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324-337.
- Gouvêa, J.B.S., L.A. Mattos and M. Hori. 1976. Fitogeografia. In: Diagnóstico Socioeconômico da Região Cacaueira: recursos Florestais. Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC) e Instituto Interamericano de Ciências Agrícolas -OEA. Ilhéus, Bahia, Brasil. 7: 1-7.
- Howe, H.F. 1984. Implications of seed dispersal by animals for tropical reserve management. Biol. Conserv. 30: 261-281.
- Howe, H.F. and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review in Ecology and Systematics 13: 201-228.
- ICMBIO. 2010. Reserva Biológica-REBIO de Una. Available at: http://www.icmbio.gov.br/brasil/BA/municipios/ilheus/rebio-de- una>. Accessed: 8/10/2010.
- Janson, C.H. 1983. Adaptation of fruit morphology to dispersal agents in neotropical forest. Science 219: 187-189.
- Janzen, D.H. 1970. Herbivores and number of tree species in tropical forests. Am. Nat. 104: 501-527.
- Janzen, D.H. 1980. Ecologia Vegetal nos Trópicos. EPU/EDUSP Temas da Biologia 7. São Paulo. pp.79.
- Kierulff, M.C.M., A.B. Rylands, S.L. Mendes and M.M. de Oliveira. 2008. Leontopithecus chrysomelas. In: IUCN 2010. IUCN Red List of Threatened Species, Version 2010.1. <www. iucnredlist.org>. Accessed: 19 June 2010.

^{*}Species whose seeds were found in faeces.

- Knogge, C. and E.W. Heymann. 2003. Seed dispersal by sympatric tamarins, Saguinus mystax and Saguinus fuscicollis: diversity and characteristics of plant species. Folia Primatologica 74: 33–47.
- Knogge, C., E.W. Heymann and H.E.R. Herrera. 1998. Seed dispersal of Asplundia peruviana (Cyclanthaceae) by the primate Saguinus fuscicollis. J. Trop. Ecol. 14: 99–102.
- Knogge, C., H.E.R. Tirado and E.W. Heymann. 2003. Effects of passage through tamarin guts on the germination potential of dispersed seeds. Int. J. Primatol. 24: 1121–1128.
- Lapenta, M.J. and P. Procópio-de-Oliveira. 2008. Some aspects of seed dispersal effectiveness of golden lion tamarins [*Leontopithecus rosalia*] in a Brazilian Atlantic Forest. Tropical Conservation Science 1: 122–139.
- Lapenta, M.J. and P. Procópio-de-Oliveira. 2009. The fate of seeds dispersed by golden lion tamarins (*Leontopithecus rosalia*) in an Atlantic Forest Fragment. Brazil. Tropical Conservation Science 2: 266–281.
- Lapenta, M.J., P. Procópio-de-Oliveira, M.C.M. Kierulff and J.C. Motta-Junior. 2003. Fruit exploitation by golden lion tamarins (*Leontopithecus rosalia*) in the União Biological Reserve. Rio das Ostas. RJ–Brazil. Mammalia 67: 41–46.
- Lapenta, M.J., P. Procópio-de-Oliveira, M.C.M. Kierulff and J.C. Motta-Junior. 2008. Frugivory and seed dispersal of golden lion tamarin (*Leontopithecus rosalia* (Linnaeus. 1766)) in a forest fragment, in the Atlantic forest, Brazil. Braz. J. Biol. 68: 241–249.
- Link, A. and A.D. Fiore. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. J. Trop. Ecol. 22: 235–246.
- Mariano-Neto, E. 2004. Efeitos da fragmentação sobre comunidades arbustivo-arbóreas em Mata Atlântica. Una BA. Phd Dissertation. Universidade de São Paulo, São Paulo. pp. 221.
- Martins, M.M. 2006. Comparative seed dispersal effectiveness of sympatric *Alouatta guariba* and *Brachyteles arachnoides* in southeastern Brazil. Biotropica 38: 57–63.
- Mcconkey, K.R. 2005. The influence of gibbon primary seed shadows on post-dispersal seed fate in a lowland dipterocarp forest in Central Borneo. J. Trop. Ecol. 25: 255–262.
- MMA. 2011. Projeto Corredores Ecológicos. Available at: http://www.mma.gov.br/sitio/index.php?ido = conteudo.monta&idEstrutura = 109. Acessed: 26/04/2011.
- Oliveira, A.C.M. and S.F. Ferrari. 2000. Seed dispersal by black-handed tamarins *Saguinus midas niger* (Callitrichinae: Primates): implications for the regeneration of degraded forest habitats in eastern Amazonia. J. Trop. Ecol. 16: 709–716.
- Oliveira, L.C., S.J. Hankerson, J.M. Dietz and B.E. Raboy. 2010. Key tree species for the golden-headed lion tamarin and implications for shade-cocoa management in southern Bahia, Brazil. Anim. Conserv. 13: 60–70.
- Passos, F.C. 1997. Seed dispersal by black lion tamarin, *Leontopithecus chrysopygus* (Primates, Callitrichidae), in southeastern Brazil. Mammalia 61: 109–111.
- Pessoa, M.S. 2008. Comparação da comunidade arbórea e fenologia reprodutiva de duas fisionomias em Floresta Atlântica no sul da Bahia. MSc Dissertation. Universidade Estadual de Santa Cruz, Bahia. pp. 81.
- Pessoa, M.S., K.M. Vleeschouwer, A.M. Amorim and D.C. Talora. 2011. Calendário fenológico: uma ferramenta para auxiliar no

- cultivo de espécies arbóreas nativas da Floresta Atlântica no sul da Bahia. Editus, Ilhéus. pp. 128.
- Poulsen, J. R., C. J. Clark and T.B. Smith. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve. Cameroon. J. Trop. Ecol. 17: 787–808.
- Procópio-de-Oliveira, P. 2002. Ecologia alimentar, dieta e área de uso de micos-leões-dourados translocados e sua relação com a distribuição espacial e temporal de recursos alimentares na Reserva Biológica União-RJ. Phd Dissertation. Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, pp. 260.
- Procópio-de-Oliveira, P., M.C.M. Kierulff and M.J. Lapenta. 2008. Dieta e área de uso de micos-leões-dourados na Reserva Bio-lógica União. RJ. In: (P. Procópio-de-Oliveira, C. Ruiz-Miranda and A.D. Grativol, eds.) Conservação do mico-leão-dourado: enfrentando os desafios de uma paisagem fragmentada. Editora da Universidade Estadual do Norte Fluminense Darcy Ribeiro. Campos dos Goytacazes. pp. 40–57.
- Raboy, B.E. 2002. The ecology and behavior of wild golden-head-ed-lion-tamarins (*Leontopithecus chrysomelas*). Phd dissertation. University of Maryland. pp. 161.
- Raboy, B.E. and J.M. Dietz. 2004. Diet, foraging, and use of space in wild golden-headed lion tamarins. Am. J. Primatol. 63: 1–15.
- Raboy, B.E., L.G. Neves, S. Zeigler, N.A. Saraiva, N. Cardoso, G. R. Santos, J.D. Ballou and P. Leimgruber. 2010. Strength of habitat and landscape metrics in predicting golden-headed lion tamarin presence or absence in forest patches in southern Bahia. Brazil. Biotropica 42: 388–397.
- Raboy, B.E., M.C. Christman and J.M. Dietz. 2004. The use of degraded and shade cocoa forests by endangered golden-headed lion tamarins *Leontopithecus chrysomelas*. Oryx 38: 75–83.
- Rylands, A.B. 1989. Sympatric Brazilian callitrhchids: the black tufted-ear marmoset. *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. J. Hum. Evol. 18: 679–605
- Rylands, A.B., M.C.M. Kierulff and L.P. Pinto. 2002. Distribution and status of lion tamarins. In: (D. G. Kleiman and A. B. Rylands, eds.) Lion tamarins: biology and conservation. Smithsonian Institution Press. Washington, DC. pp. 42–70.
- Serio-Silva, J.C. and V. Rico-Gray. 2002. Interacting effects of forest fragmentation and howler monkey foraging on germination and dispersal of fig seeds. Oryx 36: 266–271.
- Smith, A.C., H. Buchanan-Smith, A.K. Surridge, D. Osorio and N.I.
 Mundy. 2003. The effect of colour vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.). J. Exp. Biol. 206: 3159–3165.
- Souza, L.L. 1999. Comportamento alimentar e dispersão de sementes por guaribas (*Alouatta belzebul*) na Estação Científica Ferreira Penna (Caxiuanã/Melgaço/Pará). Msc Dissertation. Universidade Federal do Pará e Museu Paraense Emílio Goeldi, Belém. pp. 168.
- Stevenson, P.R. 2000. Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park., Colombia: Dispersal distance, germination rates, and dispersal quantity. Am. J. Primatol. 50: 275–289.
- Suscke, P. 2009. Padrão de atividades, dieta e uso do espaço de um grupo de *Cebus xanthosternos* (Wied-Neuwied, 1820) (Primates, Cebidae) na Reserva Biológica de Una, Bahia, Brasil. Msc Dissertation. Universidade Estadual de Santa Cruz, Bahia. pp. 132.
- Tabarelli, M. and W. Mantovani. 1999. A regeneração de uma floresta tropical montana após corte e queima (São Paulo-Brasil). Rev. Bras. Biol. 59: 239–250.
- Terborgh, J. 1983. Five New World monkeys: a study in comparative ecology. Princeton University Press, Princeton, NJ. pp. 260.

- Urbani, B. 2002. A field observation on color selection by New World sympatric primates, Pithecia pithecia and Alouatta seniculus. Primates 43: 95-101.
- Van Der Pijl, L. 1982. Principles of dispersal in higher plants. Springer-Verlag, New York. pp. 154.
- Vanderhoff, E.N. and B. Grafton. 2009. Behavior of tamarins, tanagers and manakins foraging in a strangler fig (Ficus sp.) in Suriname, South America: implications for seed dispersal. Biota Neotropica 9: 419-423.
- Wehncke, E.V., C.N. Valdez and C.A. Dominguez. 2004. Seed dispersal and defecation patterns of Cebus capucinus and Alouatta palliata: consequences for seed dispersal effectiveness. J. Trop. Ecol. 20: 535-543.
- Wehncke, E.V., S.P. Hubbell, R.B. Foster and J.W. Dalling. 2003.

- Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of Neotropical tree species. J. Ecol. 91: 677-685.
- Wrangham, R.W., C.A. Chapman and L.J. Chapman. 1994. Seed dispersal by forest chimpanzees in Unganda. J. Trop. Ecol. 10:
- Yumoto, T., K. Kimura and A. Nishimura. 1999. Estimation of the retention times and distances of seed dispersed by two monkey species, Alouatta seniculus and Lagothrix lagotricha, in a Colombian forest. Ecological Research 14: 179-191.
- Zhang, S.Y. and L. Wang. 1995. Fruit consumption and seed dispersal of Ziziphus cinamomum (Rhamnaceae) by two sympatric primates (Cebus apella and Ateles paniscus) in French Guiana. Biotropica 27: 397-401.