Seed dispersal ecology of *Leonia cymosa* (Violaceae) in the rain forest of Eastern Ecuador

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Contents **Pages**

1 Introduction

Seed dispersal is a crucial step in plant reproduction. It improves offspring survival because of escape from mortality caused by density-dependent predation and/or competition (Janzen 1970; Connell 1971; Harms et al. 2000). Long distance dispersal events enable species dispersal and colonization of distant habitat, migration of plant species, and persistence of plant populations in fragmented landscapes (Cain et al. 2000). Seed dispersal is also seen as a key process in shaping the spatial structure of plant populations via the seed shadows[1] and the seed output of individual plants. In the succession of plant regeneration processes, the so called "seed dispersal loop" (Wang et al. 2002), seed-dispersion patterns[2] are determined by the spatial pattern of reproductive adults, while in the following the pattern of future adults itself is again a result of seed-dispersion patterns (among other factors, Nathan et al. 2000; Bleher et al. 2002). Seed dispersal is also important for the maintenance of plant diversity, as indicated by spatially explicit forest models that simulate a loss of animal dispersers in a tropical rain forest (Webb and Peart. 2001).

In tropical rain forests, animal-mediated seed dispersal is a common, often the dominating dispersal mode. Up to 90% of the plants in contemporary rain forests produce fleshy fruits and depend on fruit or seed removal by frugivores and their ability to reliably disperse the seeds away from the mother plant (Howe and Smallwood. 1982; Jordano 2000). Seed dispersal of these plants can only function properly if fruit and plant traits match the sensory and morphological capacities and needs of the frugivores. Such constellations of matching fruit/fruiting traits and frugivore characteristics have been described as "fruit syndromes" (van der Pijl 1969) and "dispersal systems" (Snow 1971; McKey 1975; Howe et al. 1982). It is still controversially debated whether plant fruiting traits evolved in close interaction with frugivores (eg. in Wheelwright et al. 1982; Herrera 1985; Kalko et al. 1996; Korine et al. 2000; Schaefer 2002; Russo 2003).

This study addresses the question of whether frugivores exert selection pressures on fruits and the fruiting regime of fleshy fruited plants. I tackled the problem in a field study of the

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[1] Seed shadow: the spatial distribution of seeds dispersed from a single plant

[2] Seed-dispersion pattern: the spatial pattern of dispersed seeds, the sum of all seed shadows from all sources (Nathan, R. et al. 2000).

variation of traits of individual trees of *Leonia cymosa* (Violaceae) and the way they are linked with fruit removal from each tree. *L. cymosa* is a small tree from the under story of the Amazonian rain forest of Ecuador. I chose this small tree species from the forest undergrowth for my study, because I expected such a species to attract a smaller frugivore assemblage compared to large canopy trees, making it easier to identify the key disperser(s). Furthermore, a small tree offered better conditions to quantify the reproductive effort of the individual trees as well as the fruit removal looking at the whole tree. I chose my study species also because of the knowledge of local indigenous people about monkeys dispersing seeds of *L. cymosa*. The literature on the interaction of plants and frugivores is dominated by research on bird-dispersed plants (among the exceptions: Janson et al. 1986; Russo 2003), despite the fact that bats and monkeys are important dispersers in tropical plant communities (Howe 1986; Jordano 2000). By choosing *L. cymosa* I aimed to assess the applicability of hypotheses on frugivory to monkey-dispersed plant species.

After giving a description of the study area, the thesis is divided into two major parts that are each composed of chapters. Each chapter has its own introduction and discussion and can be read independently. In the first part, I provide detailed and comprehensive information about both sides of the interaction, the plant as well as the frugivores using the plant. The second part deals with the interaction itself.

Very little was known about *L. cymosa*'s ecology and life history, except for its geographical distribution in South America, as far as documented by specimen of botanical collections, and the discovery of an antiviral substance in its bark (Hallock et al. 2000). Therefore I present data on the tree, the spatial pattern of its population, and its fruit traits in chapter 3.1, including the analysis of macronutrients of the fruit pulp. This information is basic for understanding the seed dispersal ecology of *L. cymosa*, particularly with regard to the hypothesized dispersal systems (e.g. the specialized one and the generalized one, after Howe 1993). Then I describe the assemblage of fruit users of *L. cymosa* observed in the rainforest near the Laguna Grande de Cuyabeno, Ecuador (chapter 3.2). I characterize the nature of the relationship between each of them and *L. cymosa*, with respect in particular to their impact on fruit removal and their qualities as dispersers. I also describe the patterns of use of *L. cymosa* by monkeys.

Having thus set the frame of the plant-frugivore interactions in *L. cymosa*, I deal with feeding preferences of the main seed disperser in chapter 4.1, linking the analysis of macronutrients in the fruit pulp of individual trees with fruit removal from their crowns. This part is one of the few studies on fruit selection within a plant species.

Finally, chapter 4.2 elaborates on the question which traits of the plant and the fruit display determine fruit removal in *L. cymosa*, and whether there is evidence for selection of dispersers on any of the traits of this species.

References

Bleher, B., R. Oberrath and K. Böhning-Gaese (2002). Seed dispersal, breeding system, tree density and the spatial pattern of trees - a simulation approach. Basic and Applied Ecology **3**: 115-123.

Cain, M. L., B. G. Milligan and A. E. Strand (2000). Long-distance seed dispersal in plant populations. American Journal of Botany **87**: 1217–1227.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of Populations, Proceedings of the Advanced Study Institute on 'Dynamics of Numbers in Populations', Oosterbeek, NL, 7-18 September 1970. P. J. den Boer and G. R. Gradwell. Wageningen, Centre for Agricultural Publishing and Documentation**:** 298-312.

Hallock, Y. F., R. C. Sowder, L. K. Pannell, C. B. Hughes, D. G. Johnson, R. Gulakowski, J. H. Cardellina and M. R. Boyd (2000). Cycloviolins A-D, anti-HIV macrocyclic peptides from *Leonia cymosa*. Journal of Organical Chemistry **65**: 124-128.

Harms, K. E., S. J. Wright, O. Calderón, A. Hernández and E. A. Herre (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature **404**: 493-495.

Herrera, C. M. (1985). Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos **44**: 132-141.

Howe, H. F. (1986). Seed dispersal by fruit-eating birds and mammals. Seed dispersal. D. R. Murray, Academic Press, Australia**:** 123-189.

Howe, H. F. (1993). Specialized and generalized dispersal systems: where does 'the paradigm' stand? Vegetatio **107/108**: 3-13.

Howe, H. F. and J. Smallwood (1982). Ecology of seed dispersal. Ann. Rev. Ecol. Syst. **13**: 201-228.

Janson, C. H., E. W. Stiles and D. W. White (1986). Selection on plant fruiting traits by brown capuchin monkeys: a multivariate approach. Frugivores and seed dispersal. A. Estrada and T. H. Fleming. Dordrecht, Dr. W. Junk Publishers**:** 83-92.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. American Naturalist **104**: 501-521.

Jordano, P. (2000). Fruits and frugivory. Seeds - the ecology of regeneration of plant communities. M. Fenner, Chapman and Hall.

Kalko, E. K. V., E. A. Herre and C. O. Handley (1996). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. Journal of Biogeography **23**: 565-576.

Korine, C., E. K. V. Kalko and E. A. Herre (2000). Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. Oecologia **123**: 560-568.

McKey, D. (1975). The ecology of coevolved seed dispersal systems. Coevolution of animals and plants. L. E. Gilbert and P. H. Raven. Austin, Texas, University of Texas Press**:** 159-191.

Nathan, R. and H. C. Muller-Landau (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution **15**: 278-285.

Russo, S. E. (2003). Responses of dispersal agents to tree and fruit traits in Virola calophylla (Myristicaceae): implications for selection. Oecologia **136**: 80-87.

Schaefer, H.M. (2002) The influence of fruit pulp chemistry on avian fruit choice. Dissertation, Fachbereich Biologie, Geo- und Umweltwissenschaften, Universität Oldenburg, Oldenburg, pp 114

Snow, D. W. (1971). Evolutionary aspects of fruit-eating birds. Ibis **113**: 194-202.

van der Pijl, L. (1969). Principles of dispersal in higher plants. Berlin, Springer.

Wang, B. C. and T. B. Smith (2002). Closing the seed dispersal loop. Trends in Ecology and Evolution **117**: 379-385.

Webb, C. O. and D. R. Peart (2001). High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. Ecology Letters **4**: 491-499.

Wheelwright, N. and G. Orians (1982). Seed dispersal by animals - contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist **119**: 402-413.

2 Study area

2.1 Location, climate and forest type

Fieldwork was done in the evergreen tropical rain forest bordering Laguna Grande de Cuyabeno (0°2'N 76°15'W, elevation 250 m), located within the Cuyabeno Faunistic Reserve in north-eastern Ecuador. This area of Western-Amazonia has an annual precipitation of 3500 mm with a dry season from December to February and peak precipitations from April to June (fig. 1). A second markedly dry period usually occurs in August and September. Annual mean temperature is 26 °C.

The forest in that part of the Cuyabeno Reserve is characterized by a rich mosaic of terra firme, seasonally flooded plains of river borders and inner forest brooks and swampy areas dominated by the morete palm (*Mauritia flexuosa*). Due to strong winds, tree fall gaps are frequent. Forest canopy is at approx. 25 m. Old growth terra firme forest was shown to have a record breaking plant diversity (Valencia et al. 1994), non the less it is slightly disturbed by selective tree logging of the native population for the construction of large dugout canoes used locally.

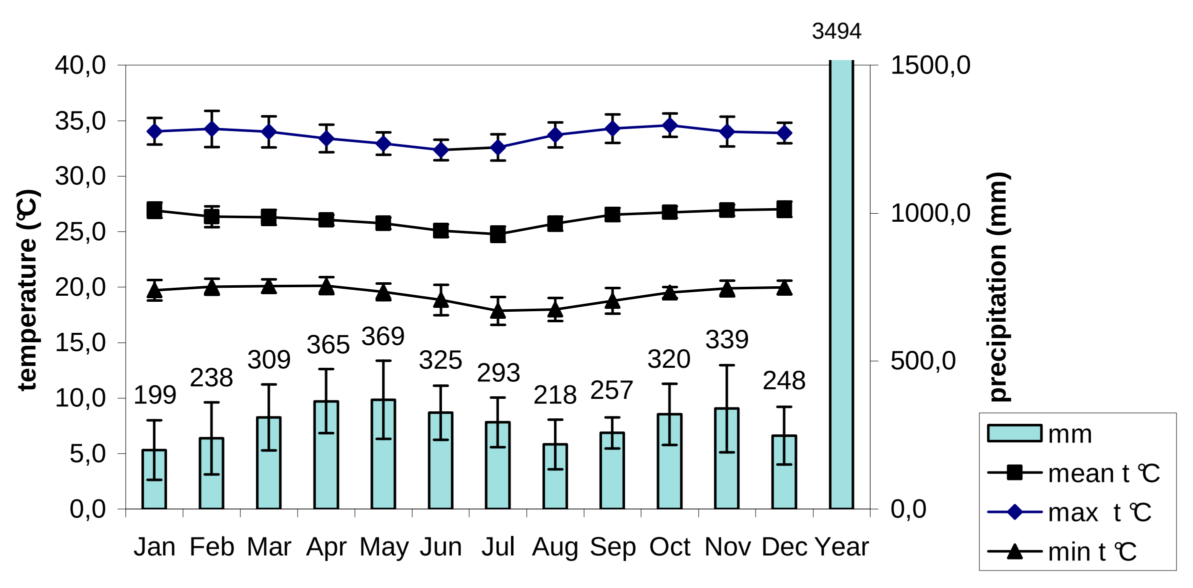

Figure 1: Climatic conditions of the study area. Mean (1981- 2000) temperatures and mean monthly precipitation at the weather station of the airport of Lago Agrio, situated ca. 80 km from the study area. Data from Dirección Aviación Civil, Quito.

2.2 Study plots

Observations and measurements focussed on four plots of terra firme forest in the vicinity of the Laguna Grande (fig. 2): **S** (“Saladero”, 6.57 ha), **J** (“Julio”, 2.78 ha), **HL** (5.53 ha) and **P** (“Palma Roja”, 6.51 ha). Study plots **S**, **J** and **P** were crossed by tourist trails. Periods of intensive fieldwork (Jan to June) fell into the low tourist season with a maximum of two guided tourist groups passing the tourist trails on some days of the week in this season.

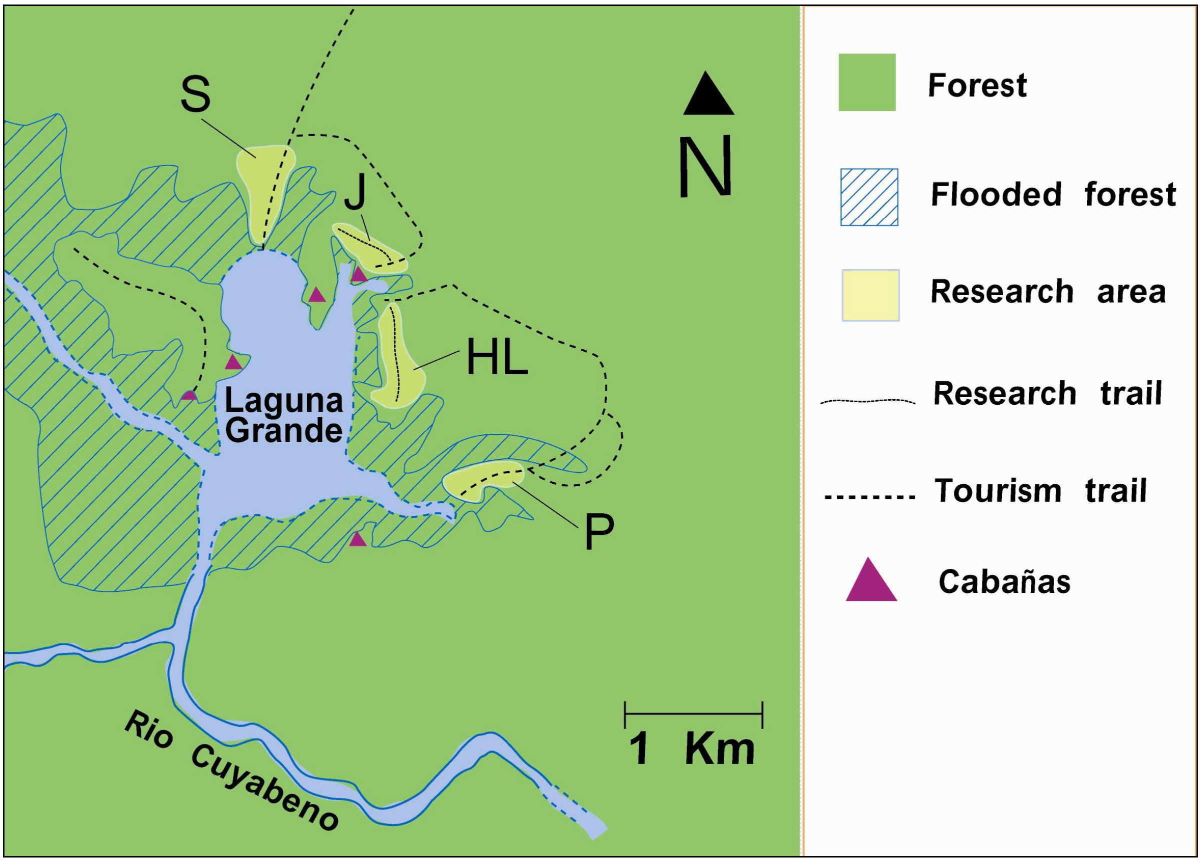

Figure 2: Location of study plots in the forest near Laguna Grande de Cuyabeno (map source: INEFAN-ONISE/OISE (1995)

References

INEFAN-ONISE/OISE (1995). Convenio para conservación y manejo ecológico en un sector de la Reserva de Producción Faunística Cuyabeno entre el INEFAN - ONISE/OISE. Ministerio de Medioambiente, Ecuador.

Valencia, R., H. Balslev and G. Paz y Mino (1994). High tree alpha-diversity in Amazonian Ecuador. Biodiversity and Conservation **3**: 21-28.

3 The Protagonists

3.1 Life history traits of *Leonia cymosa*

Abstract

The study of interaction of a fruiting tree with its frugivores requires a sound data basis on the plant's traits and the traits of its fruits. Only scarce information, mainly from botanical collections, was available on the biology of *Leonia cymosa* (Violaceae), a tree from the under storey of the rain forest of the Amazonian lowland. Here I present ecological and life history data on this tree from Ecuador, based on a four-year survey on the reproductive activity of a tree population in an old growth terra firme forest.

The mean height of a fruiting *L. cymosa* was 6.6 m (range: 2 - 12.6 m). The median tree density was 11.8 trees per ha. Trees grew in clusters consisting of different numbers of trees of different heights. *L. cymosa* flowered two times a year, in late February to March and in October. The respective fruiting seasons occurred in August/September and between March and May. The reproductive pattern is in accordance with the hypothesis that changes in sunset times at the equinoxes function as a signal triggering flower development at the Equator.

Fruits of *L. cymosa* contained the sugars fructose, glucose, and sucrose, the total soluble sugar being the first important nutritional compound of the fruit pulp. The second important compound was proteins. No lipids were found in the fruit pulp, and amino acids occurred only in traces with concentrations close to the detection limit. The variation of nutritional quality of the fruits was high within trees. Nonetheless, significant differences were found among trees in all nutrient constituents studied.

I conducted detailed fruit counts in the fruiting seasons of January to May 1999 and March to May 2000. Single trees produced a maximum of 427 ripe fruits per season. Median productivity of the trees was 45 ripe fruits throughout the fruiting season in 1999 and 36 ripe fruits in 2000. Seasonal fruit production was weakly correlated with tree size in 1999, yet not significantly correlated with tree size in 2000. The maximum standing crop of fruits in a tree was 324 fruits (counted in 2000). However, 75% of the trees had standing crops of only up to 20 ripe fruits in 1999 and up to 30 ripe fruits in 2000.

In one year, I observed a 30% loss in the overall number of fruits produced prior to removal due to infestation by lepidopteran larvae.

The traits of *L. cymosa* meet the criteria listed for a specialist dispersal system as summarized by Howe et al. (1977).

3.1.1 Introduction

In their hypothesis of generalist and specialist dispersal systems Howe and Estabrook (1977), Howe and Smallwood (1982), and Howe (1993) defined two sets of characters of tropical trees and of their respective dispersal agent. These authors contrasted “trees that produce scarce but especially nutritious fruits that entrain specialized and reliable dispersal agents, and other tree species that produce common but less nutritious fruits and appeal to individually less reliable but collectively more common species of opportunistic dispersal agents” (Howe 1993). To understand the interactions of plants with frugivores, and to find out to which extent such character sets result from selection of frugivores, it is necessary to possess a sound knowledge of the variability of the plant’s traits, such as size, fruit crop size, fruit and seed characters, and nutritional value of the fruit pulp. Only a larger sample of plants can serve as a reliable basis to study how plant traits correspond with the patterns of use by frugivores.

Leonia cymosa (Violacea), an under storey tree from the lowland tropical rain forest of Ecuador, was chosen in this study because it offered the possibility of a quantitative study of fruit production and fruit harvest for a large number of individuals. Siona indigenous people of Cuyabeno call *L. cymosa* “food of Tamarins” (“sisi e’u”; T. Criollo, personal communication). This local name, and its fruit morphology, and relatively small fruit crop sizes gave reason to expect a “specialist dispersal system” for this tree species.

L. cymosa has been frequently collected by botanists in the course of floral inventory studies as documented by the botanical database of the Missouri Botanical Garden (2005). These data points suggest a distribution of this species in the rain forest of western Amazonian near the Andes and the Guyana shield (Figure 1). Additionally, *L. cymosa* received recent interest because of the anti-viral proteins isolated from its bark (Hallock et al. 2000). However, nothing is documented about the ecology and life history of this tree. Here, I aim to characterize a population of fruiting *L. cymosa*- trees presenting data from a four year survey on the reproductive activity of these trees on the following properties:

1. size distribution and spatial pattern of fruiting trees of *L. cymosa*,
2. morphological traits and nutritional quality of its fruits,
3. flowering and fruiting seasons,
4. variation of fruit production of single trees within-years and between-years.

Figure 1: Occurrence of *Leonia cymosa* documented by botanical collection (Missouri Botanical Garden 2009). Location of study site marked with an arrow.

Thus, in this chapter I will introduce to the nature of *L. cymosa*[3] as a resource for frugivorous animals. I aim to clarify if its way to produce and display fruits fits into the "specialist dispersal system" hypothesis. Furthermore, I address the following questions: Do individual trees show a specific nutritional quality of their fruits that would allow frugivores to make a choice between individual trees? Are there reliable "prime fruit producers" among the trees that could be memorized by frugivores?

My findings also form one of the rare long-term data sets on the reproductive activity of trees growing at the Equator. At the Equator the question of flower induction is still unsolved because day length is constant throughout the year and thus the photoperiodic control of plant development known from higher latitudes does not work here. I will

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[3] *Leonia cymosa* Mart., Herbarium QCA of the Pontifícia Universidad Católica del Ecuador in Quito, specimen No. 14, 2001, Albrecht Pfrommer

examine if the patterns of flowering and fruiting found in *L. cymosa* allow concluding on new mechanisms of photoperiodic time keeping proposed by Borchert et al. (2005).

3.1.2 Size distribution and spatial pattern of fruiting trees

3.1.2.1 Methods

Mapping techniques and measurements of trees

Preliminary surveys showed that *L. cymosa* starts fruiting with a height of about 2 m. This observation is confirmed also by indigenous knowledge (T. Criollo, personal communication). In order to locate all fruiting trees in my study plots I mapped all *L. cymosa* with a size of 2 m and bigger. To find these trees it was not necessary that they fruited or flowered, because even at infertile stage trees of *Leonia cymosa* can be identified easily by their characteristic slightly serrate leaves and their irregularly curved thin trunks. The complete population of *L. cymosa*-trees of 2 m height and larger was mapped at the study sites **HL**, **J**, **P**, and **S** (see map in chapter 2, figure 2), within a total study area of 22 ha, using an ultrasonic pulse-echo distance measurer (Sonin Pro) and a compass (Eschenbach). Distance values and angles served to produce a digital map with a fully functional test version of AutoCAD 2002 (Autodesk). This initial map (in AutoCAD format) was transferred to ArcView (ESRI) for further spatial analysis and printing of maps.

Tree density of *L. cymosa* per hectare was calculated based on the total searched area, as determined from polygons in the ArcView-maps. The study area was searched thoroughly and repeatedly for *L. cymosa*-trees. All big individuals in the area were identified. However, it cannot be ruled out that some of the smaller individuals were missed.

Tree height was measured with a “Spiegelrelaskop” (FOB, Salzburg, Austria), an optical precision instrument that permits reading tree height by focusing on the highest point of the crown periphery from a known distance.

To measure crown volume I decided first which geometric body (like cube, sphere, cone, tetraeder, etc.) would best fit the shape of the tree’s crown. I then took the necessary key measurements and calculated the tree’s volume according to standard geometric formulas.

3.1.2.2 Results

Tree density and spatial distribution

The density of *L. cymosa* showed large variation in the four study plots (Table 1). Median tree density per hectare was 11.8 trees. Trees were found in clusters (Figure 2) of different tree sizes. However, a tendency of trees to grow up locally in cohorts could also be seen.

Table 1: Densities of *L. cymosa* >2 m in four study sites

Study site code	HECTARES	No of –trees	density (trees/ha)
HL	5.53	64	11.6
J	2.78	64	23.0
P	6.51	78	12.0
S	6.57	25	3.8

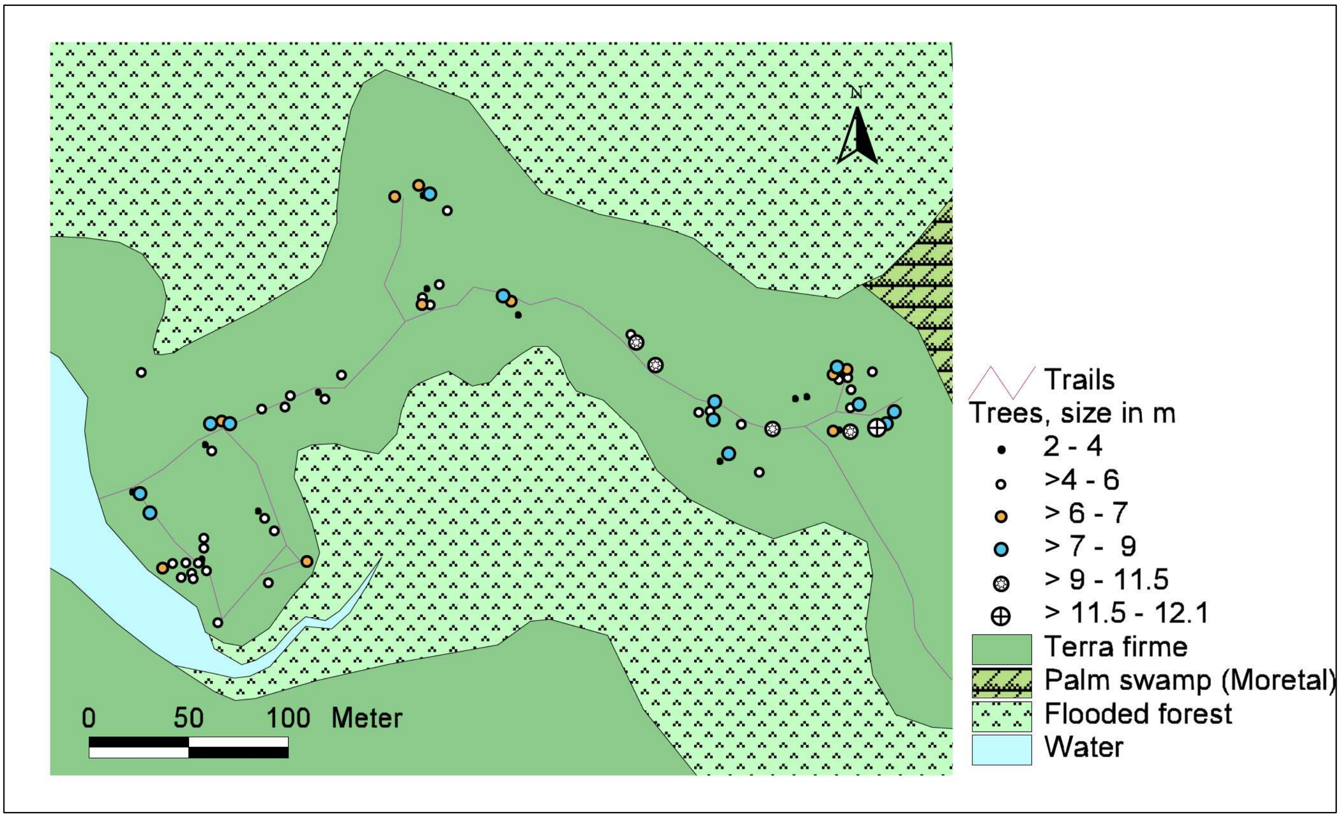

Figure 2: Map of trees > 2m in plot **P** (Palma Roja)

Size and crown volume of fruiting trees

The height distribution of 306 fruiting trees of *L. cymosa* follows a normal distribution (Figure 3; n=306, K-S d = 0.05026, p> 0.20; Lilliefors p<0.10), although slightly skewed to smaller trees with a mean tree height of 6.6 m (SD = 1.91). The smallest fruiting tree found in the area was 2 m high and the tallest individual measured 12.6 m in height. Crown volume was significantly correlated with tree height (Figure 4, Spearman rank correlation, n=85, R=0.528, p<0.001). However, it is noticeable that crown volume remains small in many trees over a wide range of heights. Thus, trees in the upper third of the height range may still have small crowns.

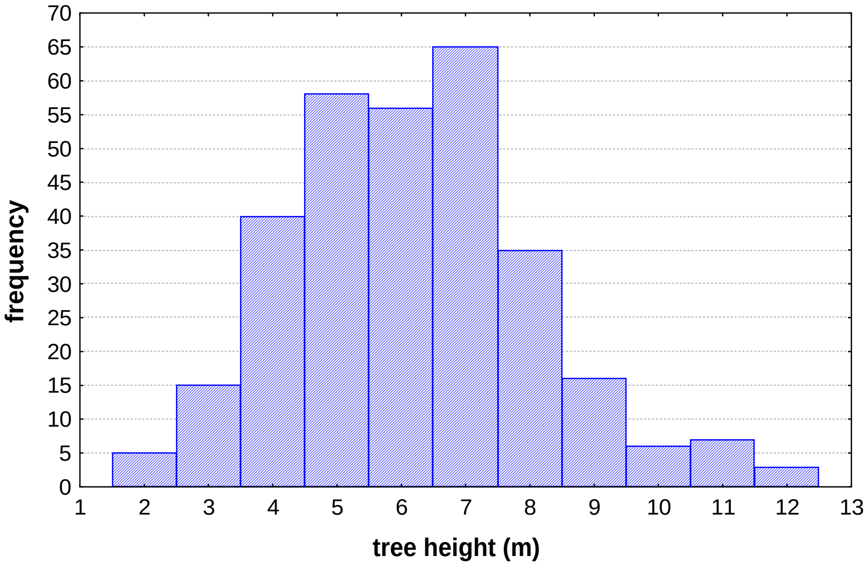

Figure 3: Frequency distribution of height (m) of fruiting *L.cymosa* trees (n=306)

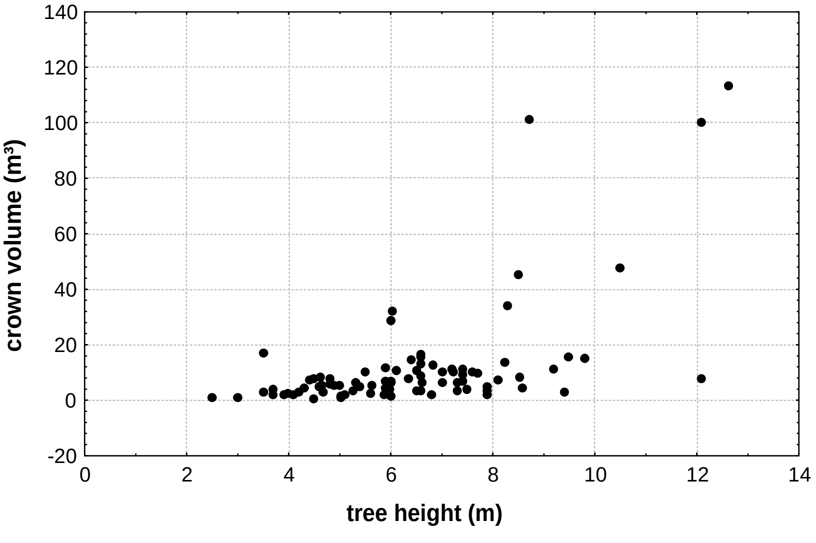

Figure 4: Correlation of tree height and crown volume

3.1.3 Flowering and fruiting seasons

3.1.3.1 Methods

Between August 1998 and May 2001 I monitored the flowering and fruiting activity of 34 focus trees from all four study plots. Focus trees were selected to be of a minimum height of 5 m and to be distributed evenly over the study plots in order to cover a large area of the forest near Laguna Grande de Cuyabeno.

Yet, the first fruiting event was already documented in 1997, during preliminary research from August to October. Focal trees were visited every month from August 1998 to June 1999 and afterwards in the following months: 8/99, 1/00, 3/00, 7/00, 10/00, 4/01. During surveys I noted the presence / absence of buds, flowers, green fruits, and ripe yellow fruits.

3.1.3.2 Results

Two periods of flowering occurred in *L. cymosa* each year, one in late February to March and one in October, each lasting about one month. The October flowering event was directly observed only in 1998 (Figure 5). However, it must have occurred in all years of this study. This can be concluded from the presence of small green fruits in January 2000, and also from the development of green and ripe fruits in April 2001. 91% of the focus trees flowered during October 1998, whereas only 23% flowered during February/March 1999.

After flowering, it took approximately 2 months until tiny green fruits had developed, and another 3 months passed until fruits reached their final size and ripening ensued. Within an individual tree fruits matured in an asynchronous fashion, i.e. only a small proportion of all fruits present in a tree crown ripened while the others were still green. In accordance with the two flowering events, I observed two fruiting seasons per year, the first between March and May and a second one in August to September.

The first fruiting season in each year varied in duration between 2 and 4 1/2 months, with a phase of intensive fruit ripening in April. I observed this pattern in three consecutive years (1999-2001). The second fruit season in August/September seemed to be more variable in onset, duration and occurence, as can be seen when comparing the year 1999 with the year 2000. In August 1999 fruit ripening had not yet started, while in August 2000 the proportion of trees with ripe fruits had already reached its peak. Also, in 1997 *L. cymosa*-trees fruited from August to October whereas in 1998 no fruiting occurred at all at that time of the year.

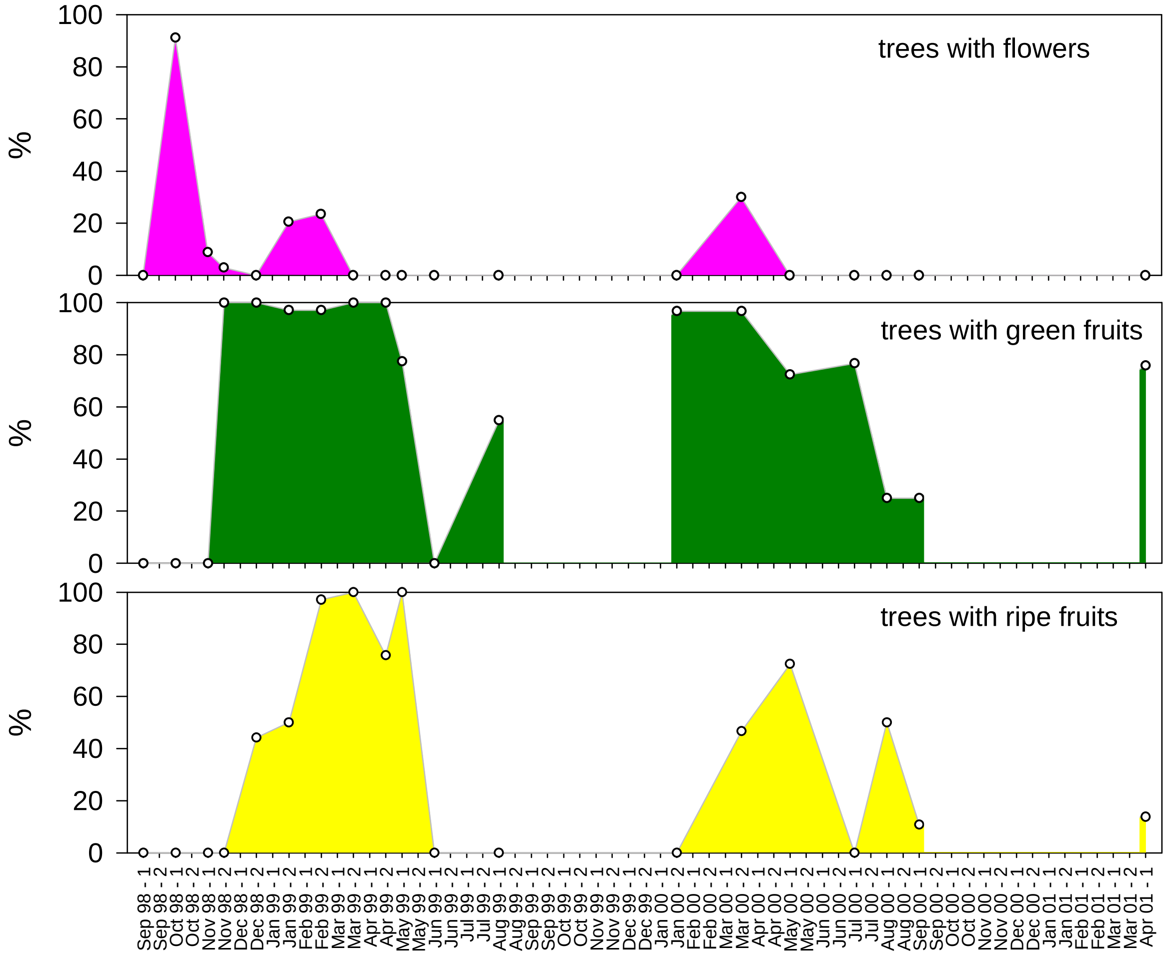

Figure 5: Flowering and fruiting periods 1998-2001 (based on 34 trees). Open circles indicate dates of control.

3.1.4 Fruit morphology and nutritional quality

3.1.4.1 Methods

Sampling fruits

I collected 10 ripe, yellow fruits each from 12 individual trees. In order to characterize the nutritional status of yellow-green fruits, which are not yet fully ripe, but already attractive for frugivores, I collected an additional 10 yellow-green fruits each from 2 of these trees.

Within the respective ripeness category, the fruits sampled were of similar size and similar properties (color, softness) and were picked from different branches of a tree. All fruit samples were collected in May 2000. Only large trees with a large number of fruits were sampled in order not to interfere with the study of fruit removal by frugivores.

Fruit pulp and seed mass

I measured the diameter of the fruits, separated the pericarp from the fruit pulp and seeds and weighed the fruit pulp-seed-compound with a Mettler PJ 300 balance (accuracy: 0.001 g). I separated seeds from fruit pulp, counted them, and measured the fresh weight of fruit pulp. Total seed mass (fresh weight) per fruit was calculated by subtracting fruit pulp weight from the weight of the pulp-seed compound.

Nutritional analysis of the fruit pulp

Preparation of pulp samples

Fruit pulp was conserved in the field in approx. 5-7 ml ethanol (98%) in 10 ml-scintillation bottles of known tare weight. In the laboratory fruit pulp samples were dried inside the scintillation bottles by blowing dry air for 7 days through canulas into the bottles evaporating the ethanol. Samples were then further dried inside a drying closet at 35-40°C until weight remained constant. Dry weight of the fruit pulp samples was eventually determined by subtracting the weight of the bottles.

Subsequently, I added between 5 and 15 ml of double-distilled water to the dry fruit pulp (approximately 5 ml per 1.5 g fresh weight of fruit pulp). In this water the pulp was homogenized with an ULTRA-TURRAX®. The homogenate was then used for further analysis.

Sugars

0.5-1.0 ml of homogenate of each fruit pulp sample was transferred into an Eppendorf tube. E-tubes and remaining homogenates were stored in a freezer at -22°C. After thawing, the homogenate was centrifuged in the e-cup for 5-10 min at 13000 rpm. 20 µl of the clear supernatant were separated and analyzed by high pressure liquid chromatography (HPLC) for sugar contents (pump and degasser: Knauer, column: Stability Polyamine L.D., 250 x 4,6 mm, grain size 5 µm, by Dr. Maisch High Performance GmbH, Ammerbuch, Germany; mobile phase: acetonitrile:water 80:20; RI-detector: ER C 7510, Erma Optical Works, Ltd.). Two successive analyses per extract sample were run and showed very little variation in the resulting chromatogram. Mean peak areas of both runs were used to calculate the concentration of the different sugars, calibrated by a serial dilution with 0.01878 – 0.0375 – 0.075 – 0.15 – 0.3 mg/20 µl of a stock solution of 30 mg/ml fructose, glucose and sucrose (p.A.) in HPLC grade water.

Protein

100 µl of fruit pulp homogenate were transferred into a previously weighed E-tube and the E-tube was weighed again. 1000 µl 0.1 M NaOH were added, the sample was mixed thoroughly using a Whirl-Mix and stored overnight for extraction. The homogenate was then centrifuged in the E-tube at 10000 rpm. 10 µl of the clear supernatant were added to 90 µl of distilled water and 1 ml of a fresh dilution (1:50 in distilled water) of BCA Protein Assay Reagent (Laborchemie GmbH, St.Augustin) and this mixture was then incubated in a water bath at 37 °C for 30 min. After letting it cool down to ambient temperature, extinction of the mixture was measured at a wavelength of 562 nm with a Carl Zeiss spectral photometer (Monochromator M4 Q II, display equipment PM Q II). 0, 10, 20, 30 and 40 µl of a 1mg/ml BSA solution with distilled water added, to complete 100 µl, were used to produce a calibration curve.

Protein content was calculated as follows:

mg protein / g dry weight =

$$\frac{\text{mg protein } (\mu\text{g protein}/1000) * 1000\ \mu\text{l Na OH} * \text{g (volume of original homogenate; g = ml)} * \text{dilution factor}}{10\ \mu\text{l (supernatant)} * \text{g (weighted homogenate sample)} * \text{g dry weight of orig. pulp sample)}}$$

Three replicate analyses were carried out for every fruit pulp sample. A mean was calculated from these replicates to obtain the result for one individual sample.

Amino acids

To search in a cost-friendly manner for soluble amino acids in the fruit pulp of *L. cymosa* I prepared a sub-sample of fruit pulp homogenate for amino acid analyses. 100 µl of fruit pulp homogenate of only one fruit of each of the trees sampled were pipetted into a previously weighed E-tube, the E-tube was weighed again, 1 ml of H_2O was added and the solution well mixed. Proteins were precipitated by keeping the E-tubes for 5 min in a water bath at 100 °C. Afterwards samples were immediately cooled on ice and centrifuged for 20 min at 5000 rpm. 75 µl of the supernatant were combined with 75 µl of a tri-Lithium citrate-citric acid buffer solution (0.1 n Li, 0.0685m citrate, pH 2,2) in special cups for amino acid analyses and samples were stored deep frozen until separation and measurement of amino acids with an Amino Acid Analyser I 5001 (Biotronic, Maintal, Germany) against a calibration standard solution (Benson Company, Reyno) and freshly prepared standards of L-Glutamine L-Asparagine.

Amino acid (AA) content was calculated as follows:

mg AA/g dry weight =

$$\frac{\mu\text{M AA} * 1000\ \mu\text{l } H_2O * \text{g (volume of original homogenate; g = ml)} * \text{dilution factor}}{1000\ \text{ml} * \text{g (weighted homogenate sample)} * \text{g (dry weight of orig. pulp sample)}}$$

Lipids

The conservation of the fruit pulp in ethanol itself functioned as an extraction method for lipids from the fruit pulp. When ethanol was evaporated, any lipids should have remained at the walls and on the floor of the vials. Indeed, a sticky brownish-yellow extract was found at the ground of the dried scintillation bottles, but this extract was completely soluble in water. Weighing the bottles showed that no other substances insoluble by water remained in the vials. Therefore I concluded that the fruit pulp did not contain any lipids or only minimal amounts below the threshold of detection with my methods.

Water content

The water content of the fruit pulp was calculated by subtracting dry weight from fresh weight of fruit pulp. Water content was expressed in percent fresh weight.

3.1.4.2 Results

Morphological traits of flowers and fruits

L. cymosa had tiny yellow-whitish flowers of about 2-4 mm size that grow in clusters (see Figure 6). I observed a large number of stingless bees (Meliponinae) when I climbed tree crowns during flowering, but none during other reproductive states. Thus, Meliponinae are probably important pollinators of *L. cymosa*.

The fruit that grows from the pollinated flower is a berry (= a fruit with seeds immersed in pulp), spherical in shape, 13 to 30 mm in diameter (sometimes up to 40 mm), with a thick, woody epicarp (Figure7). Fruits grew in clusters or alone, each on a short leafless twig (2-3 cm) while their fruiting pedicel was only about 3 mm long. Unripe fruits had a dark green color and their pericarp could not be separated from the pulp-seed compound. Ripeness was indicated by a softer pericarp that could be easily detached from the seed-pulp-compound, by a sweet taste of the fruit pulp, by fully developed seeds, and by a change of color. I distinguished two stages of ripe fruits, namely “recently ripened fruits” and “fully ripe fruits”. Recently ripened fruits were light green to yellow in color, whereas fully ripe fruits were pale yellow. Both were consumed by frugivores. Both ripening stages contained white to yellow pulp that was sticky and tightly connected to the seed. Therefore I could only separate it from the seed by using preparation instruments. It should be very difficult for frugivores, either, to separate pulp from seed in order to get rid of the seeds before devouring the pulp.

Depending on their size, fruits contained from 1 to 12 oval to reniform seeds which measure 13 mm in average length (range: 10-15.5 mm, n = 18). The median of the mean seed weight of 137 sampled fruits was 0.45 g (minimum: 0.125 g, maximum 0.75 g, mean seed weight of a fruit calculated as total weight of seeds divided by the number of seeds of that fruit). The number of seeds was highly correlated with the size of sampled fruits ($r^2 = 0.57$, $p < 0.001$, n = 27). The absolute weight of pulp per fruit increased with the number of seeds up to 5 seeds, then the curve flattens (Figure 8; n = 117, Adjusted $R^2 = 0.47$, F = 102.6 , $p < 0.0001$, $y = 0.48 + 0.687*\log10(x)$). However, the pulp mass to seed mass ratio, which better reflects the pulp gain of a frugivore relative to handling cost, was not correlated with number of seeds, i.e. it did not increase with fruit size (Figure 9, Spearman rank correlation, n = 117, R = 0.09, p = 0.312).

Figure 6: Position of flowers of *L. cymosa*. Flower buds are still closed here. Their diameter is about 2-3 mm.

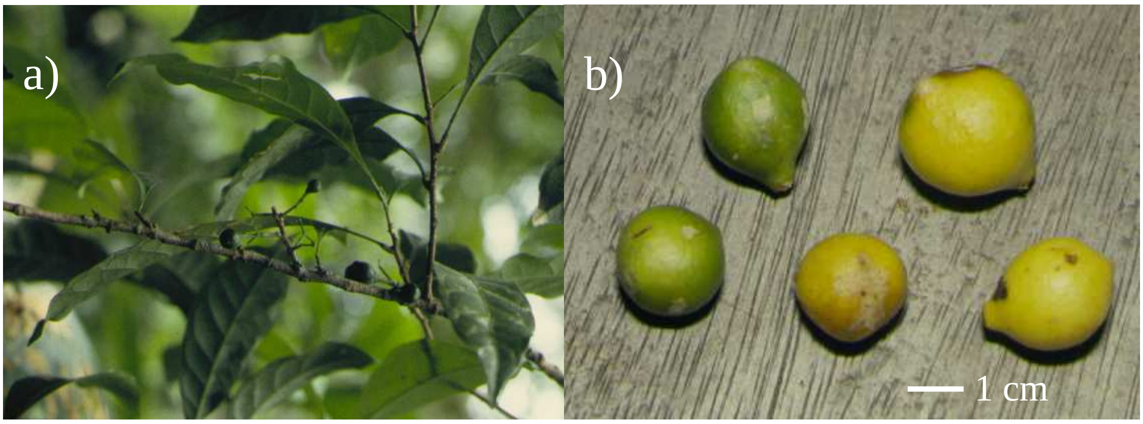

Figure 7: a) Green fruits on a twig of *L. cymosa*, b) Green to yellow and final yellow stage of fruit ripeness.

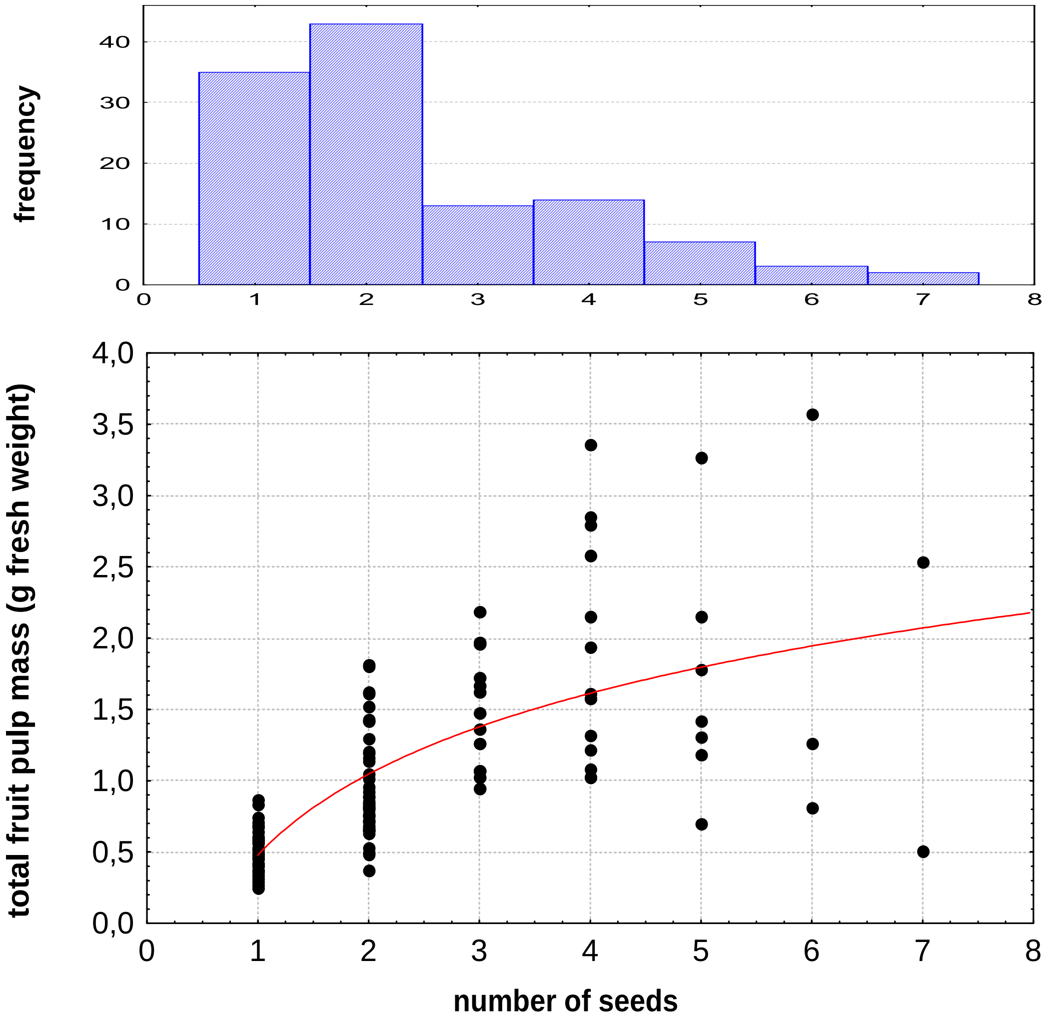

Figure 8: Correlation of total pulp mass and number of seeds per fruit.

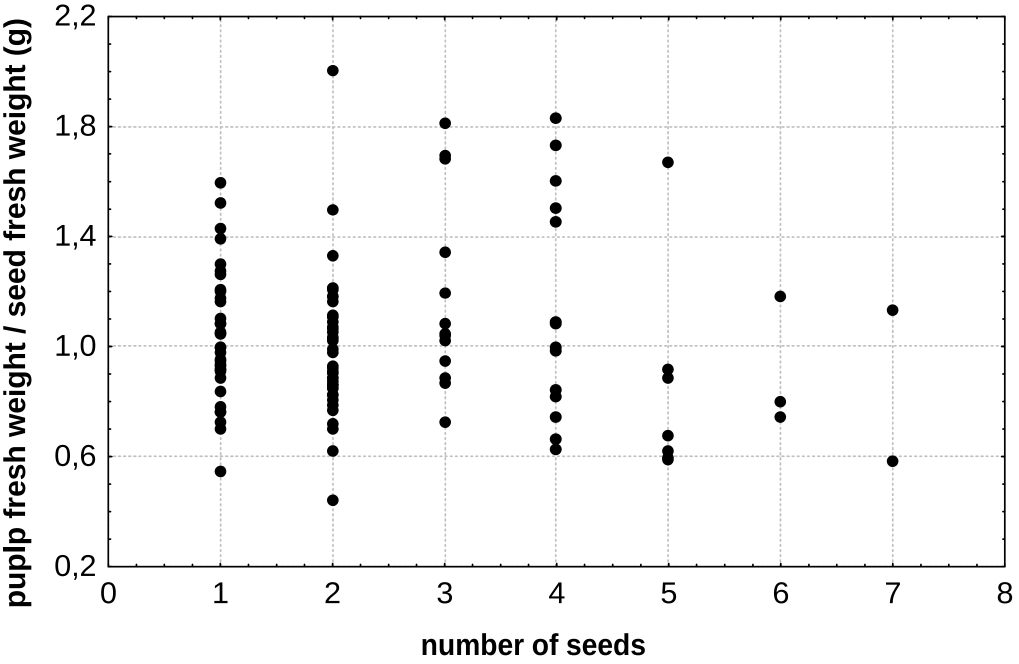

Figure 9: Correlation of ratio of pulp to seed fresh weight with number of seeds per fruit.

Nutritional composition

The fruit pulp of *L. cymosa* contained mainly sugar, protein and water. Soluble sugars accounted for about half of the dry weight (DW) of the fruits of *L. cymosa* (Table 2). Sugars found in the fruit pulp were fructose, glucose and sucrose. The median content of these sugar components in the fruits of individual trees ranged from 97 to 249 mg/g DW fructose, from 120 to 275 mg/g DW glucose and from 11 to 361 mg/g DW sucrose (median of the fruits sampled from a single tree). The median of the total amount of soluble sugars ranged from 415 to 642 mg/g DW. The second most important nutritional compound of the fruit pulp was protein which accounted for approximately a fifth of the dry weight. Medians of protein content of the fruits from individual trees ranged from 129 to 235 mg/g DW of fruit pulp. Amino acids were found in very low concentrations close to the lower detection limit (for values see appendix A). Only traces of Alanine and Glutamic acid were found with reliable chromatogram peaks in more than half of the samples, in amounts of a maximum of 7.2 µmol/g DW Alanine and 7.9 µmol/g DW Glutamic acid.

No lipids were found in the fruit pulp. The remaining dry matter of the fruit pulp (components insoluble in water) consists of ashes and cellulose. Both were not analysed in detail.

Table 2: Nutritional composition of the fruit pulp of fully ripe (yellow) fruits of *L. cymosa*.

	Mean (n = 105)	Minimum	Maximum
water content (% fresh weight)	76.5	66.4	83.1
total soluble sugar (% dry weight)	53.2	21.3	73.6
protein (% dry weight)	18.6	10.7	28.9
insoluble dry matter (ashes and cellulose)	28.1	5.1	61.3

Variation of quality among and within individual trees

By having collected only fruits of similar size and properties throughout all trees sampled, I could make sure that only fruits of the same stage of ripeness were analysed. Still, there was a great variation within trees as well as between trees in the content of nutrients in the fruit pulp, in the water content, and in the mass of fruit pulp relative to the seed mass (Figures 10 to 13). At the date of fruit sampling, each tree showed a specific pattern of concentration of sugars contained in its fruit pulp (Figure 10). Significant differences were found between trees in all nutrient constituents studied (see table 3 for the results of overall tests for differences between trees). Figure 10 reveals an inverse relationship between the content of fructose and glucose on one hand and sucrose on the other hand: high fructose and glucose contents are associated with low sucrose content and vice versa.

Table 3: Between-tree comparison of 12 trees of *L. cymosa*. Results of Kruskal-Wallis-ANOVAs of nutrient contents.

	Kruskal-Wallis H	P	df ; N
Fructose	61.9	< 0.001	11; 118
Glucose	61.9	< 0.001	11; 118
Sucrose	83.4	< 0.001	11; 118
total soluble sugar	49.2	< 0.001	11; 118
Protein	56.8	< 0.001	11; 114
Water content	70.5	< 0.001	11; 118
Fruit pulp / seed	83.1	< 0.001	11; 117

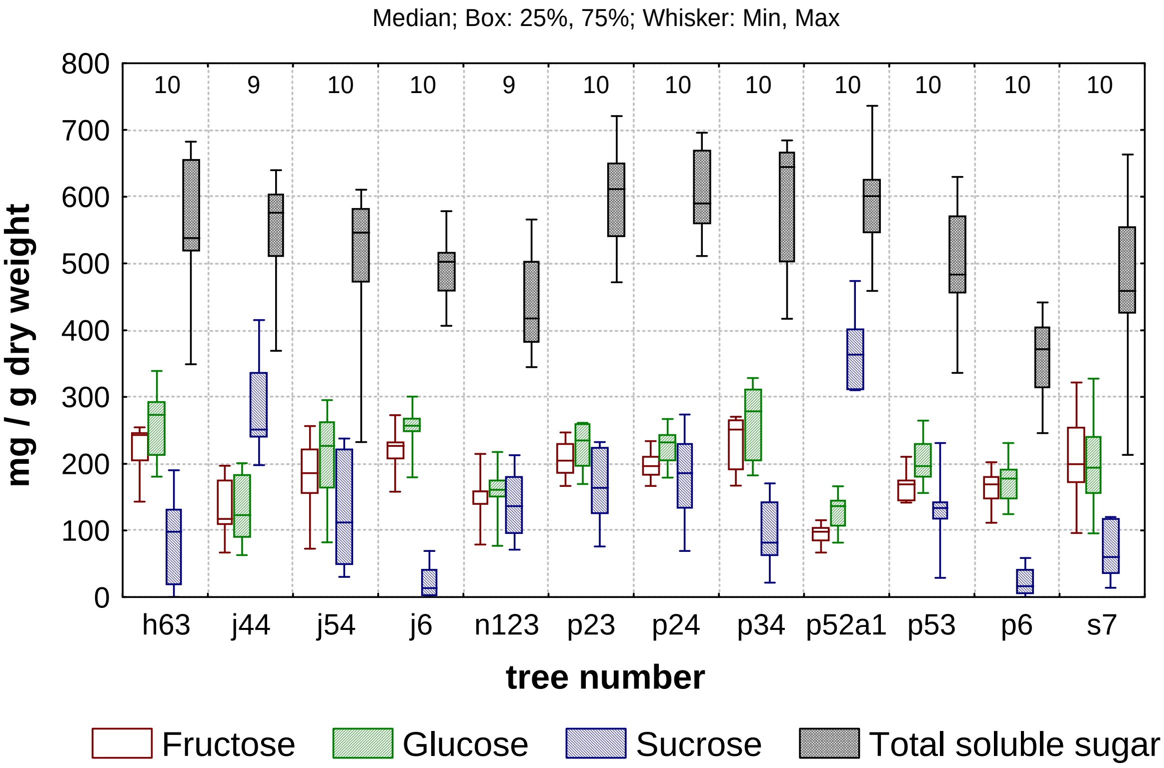

Figure 10: Sugar content of the fruit pulp of fruits from 12 trees of *Leonia cymosa*. The number of fruits analysed per tree is given above the box plots.

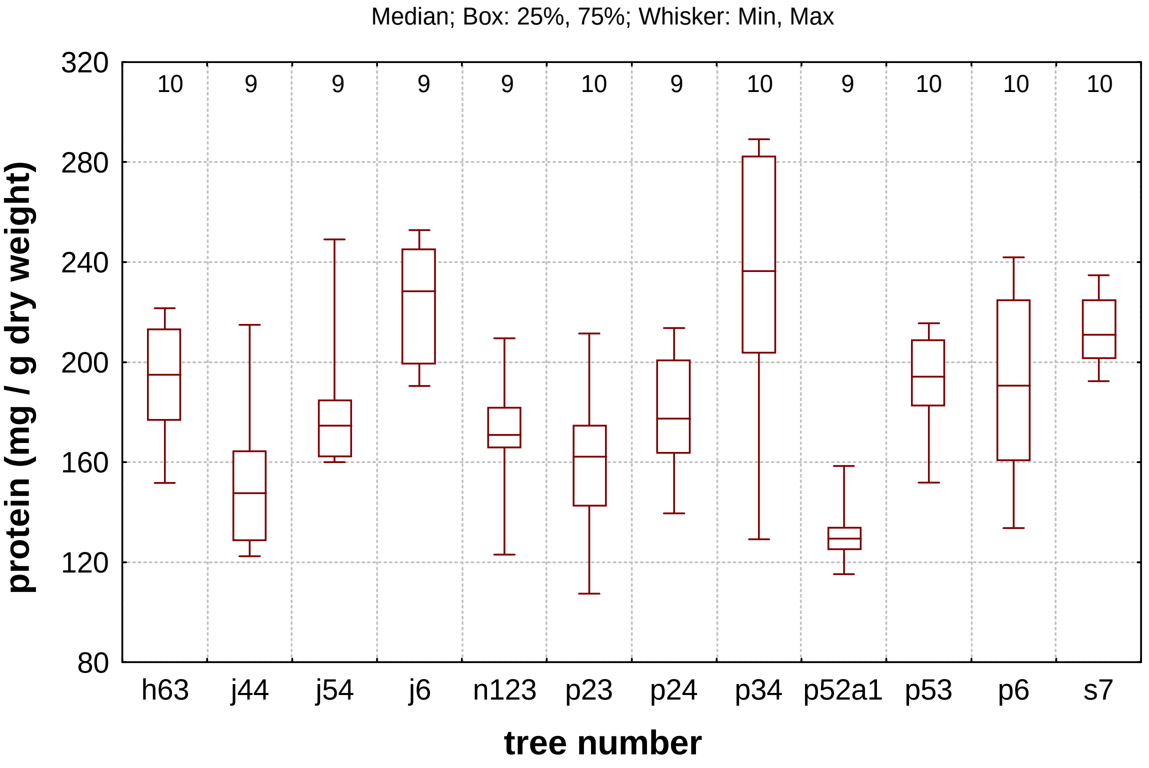

Figure 11: Protein content of the fruit pulp of fruits from 12 trees of *Leonia cymosa*. The number of fruits analysed per tree is given above the box plots.

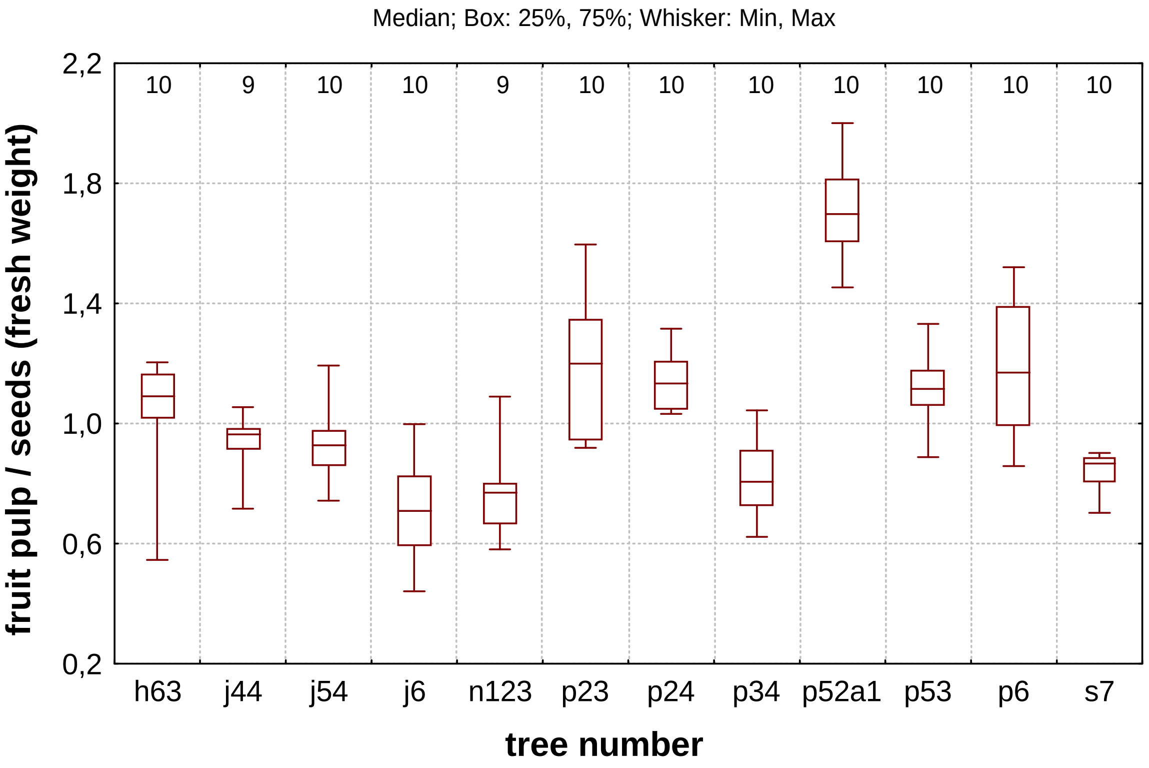

Figure 12: Fruit pulp to seed ratio of fruits from 12 trees of *Leonia cymosa*. The number of fruits analysed per tree is given above the box plots.

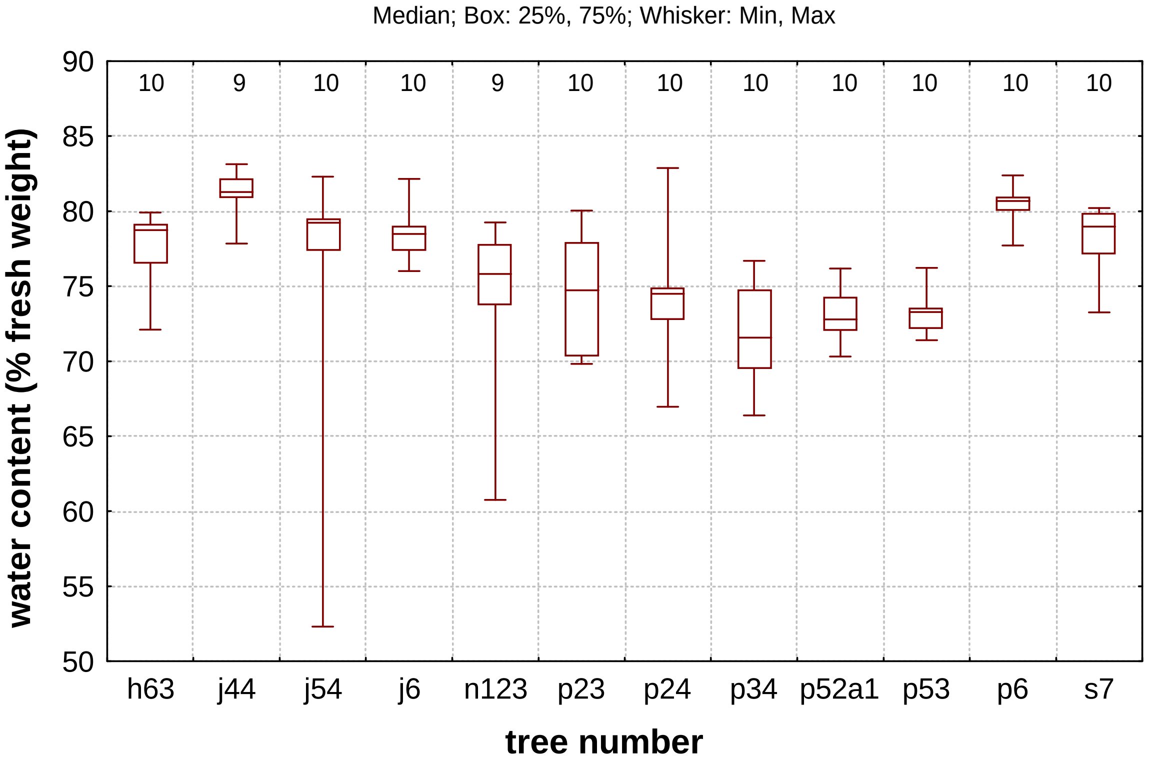

Figure 13: Water content of the fruit pulp of fully ripe (yellow) fruits from 12 trees of *Leonia cymosa*. The number of fruits analysed per tree is given above the box plots.

Two stages of fruit ripeness compared

Fruits of *L. cymosa* change color in the course of fruit ripening: from dark green (= unripe) to light green to yellow (recently ripened) to yellow (= fully ripe). Frugivores were observed to take both green to yellow and yellow fruits. Indeed, in the two trees sampled, green to yellow fruits already showed the tree-specific sugar composition found also in yellow fruits from of the same tree (Figure 14). Likewise, no differences between the two stages of ripeness of fruits from the same tree were found with respect to protein (Figure 15, Mann-Whitney U = 30.0 Z = -1.22474, p = 0.22, n =9) and the pulp weight to see weight ratio (Figure 16). A significant difference in water content between green to yellow and yellow fruits was found only in one tree (Figure 17, Mann-Whitney U = 11.0, Z = 2.95, p = 0.003, n = 10).

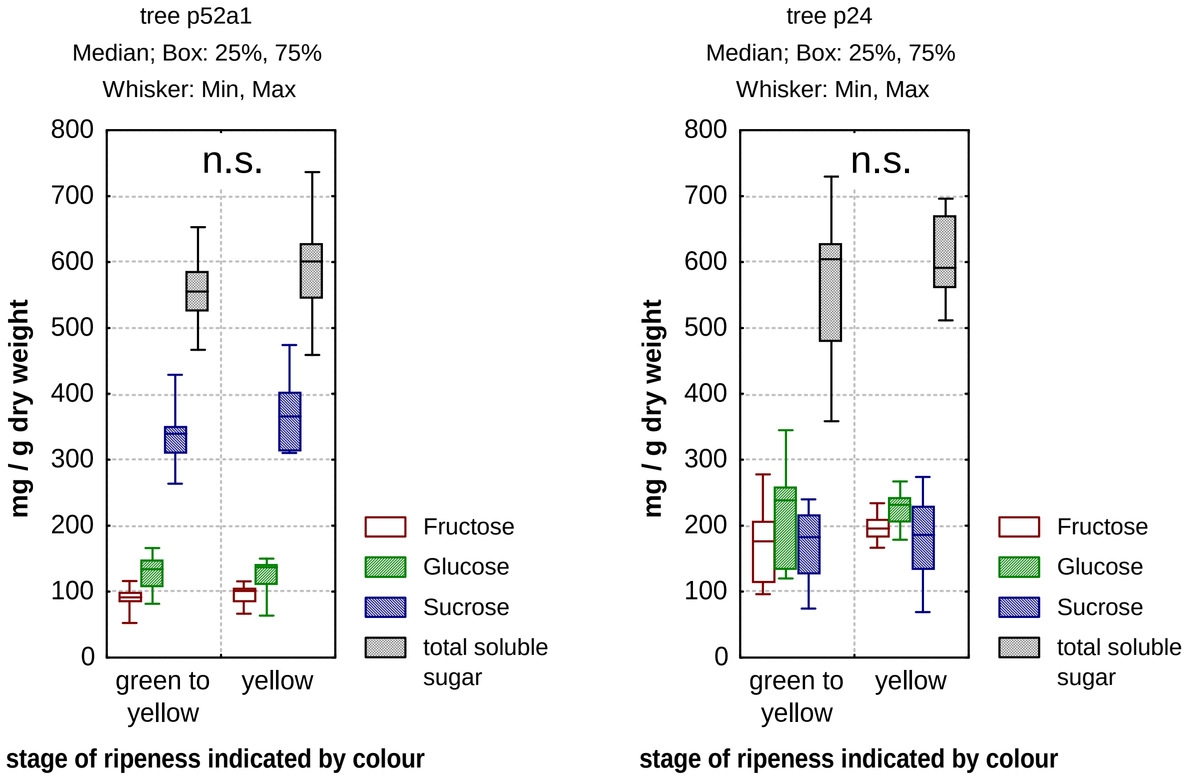

Figure 14: Sugar content of the fruit pulp in two subsequent stages of fruit ripeness. Green to yellow color indicates recently ripened and yellow color indicates fully ripe fruits.

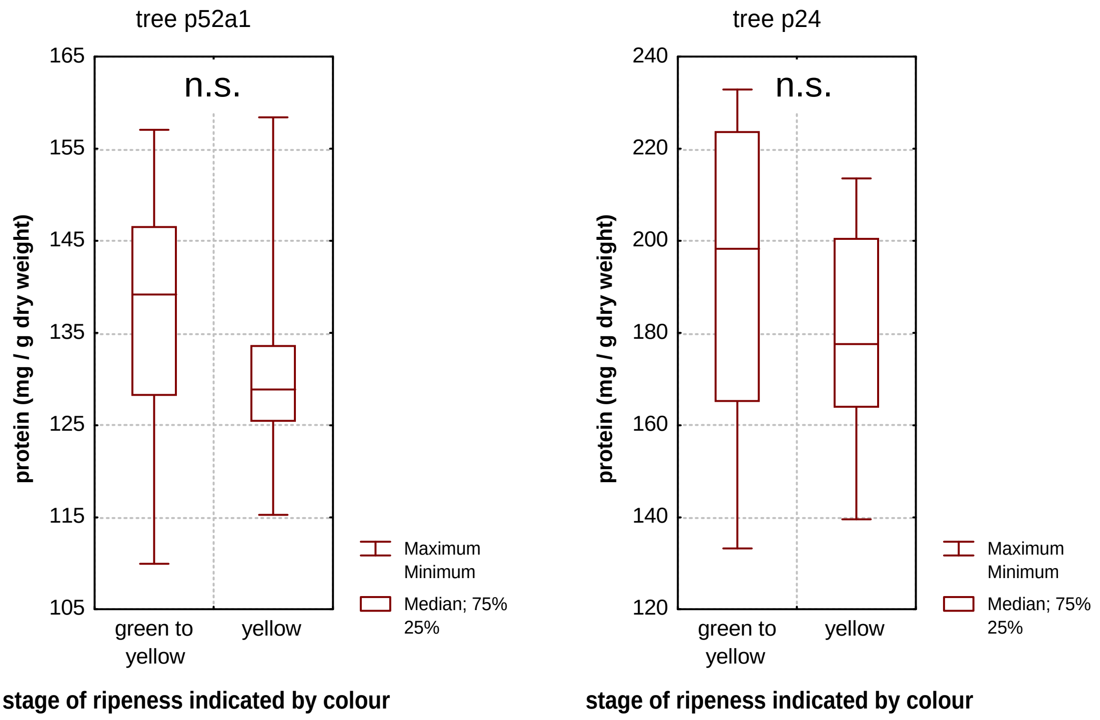

Figure 15: Protein content of the fruit pulp in two subsequent stages of fruit ripeness.

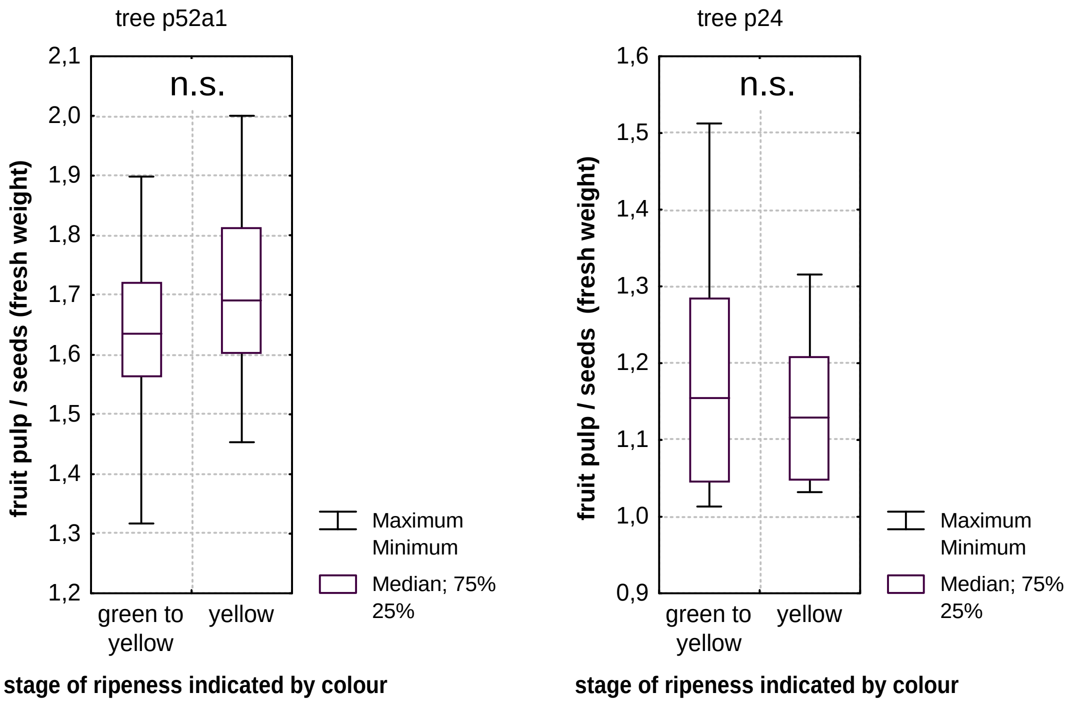

Figure 16: Fruit pulp to seed ratio of fruits in two subsequent stages of ripeness.

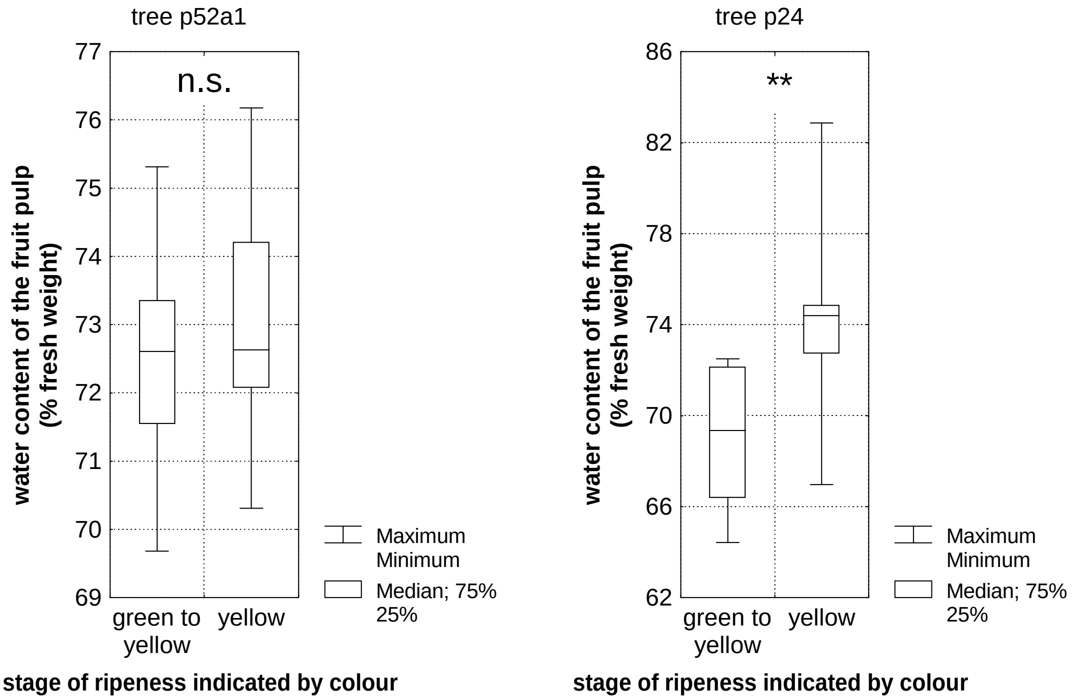

Figure 17: Water content of the fruit pulp in two subsequent stages of fruit ripeness.

3.1.5 Individual fruit production: variation within years and between years

3.1.5.1 Methods

Fruit counts in 1999

In December 1998, when trees started to produce green fruits, a total of 61 individuals were selected from study sites **HL**, **J**, **P** and **S** representing the whole size range of *L. cymosa*-trees and the whole range of potential fruit crop sizes. I placed olive green mosquito nets in about 1 m height covering the crown area underneath each of these trees with as little disturbance of the undergrowth vegetation as possible. From end of December 1998 to May 1999 – when the fruiting period finished – all fully grown green and all ripe fruits in the tree crowns, and all fruits or peels of fruits found in the net underneath a tree were counted biweekly. Two stages of fruit ripeness were differentiated by color and counted separately: an earlier yellow-green stadium and a later yellow stadium. It was possible to count the number of fruits from the remaining peels because peel (pericarp) fragments were large and points of connection to fruit stems could be identified clearly.

I used a 4 m aluminium ladder to access tree crowns. Fruits of a few large individuals were counted by climbing into their crown or on branches of neighbouring trees. Counts were enabled by a variety of hooks to get hold of single branches and by handheld tally counters. Large trees with dense foliage were counted by two persons, one counting and one assisting in separating branches. As fruits of *L. cymosa* are large and as we initiated re-counts at the slightest suspect of an error in counting, counts can be considered accurate.

Fruit counts in 2000

During the fruiting period of 2000 from End of March to May, the complete fruiting tree population of the study plots **HL** and **P** (in total 93 trees of *L. cymosa*) were included in weekly fruit counts (intervals ranged from 6-8 days). I applied a counting technique similar to that in 1999, but I did not use nets to catch fruits falling from the crowns. Instead, I checked all trees daily for peels of fruits and for entire fruits on the ground from 12th of April to 10th of May. When peels were found, the number of consumed fruits was counted as described above, and the ripe fruits remaining in the tree crown were counted to determine the degree of depletion by visiting monkeys.

Calculations for quantifying fruit production

As described, surveys of fruiting trees during the fruiting periods of 1999 and 2000 resulted in a series of counts that can be schematically illustrated like:

$$\text{count 1} \overset{\text{interval 1}}{\text{----------------------}} \text{count 2} \overset{\text{interval 2}}{\text{----------------------}} \text{count 3 ...}$$

I calculated the production of ripe fruits (P) of a given tree during a given interval according to the following simple equation (here exemplified with “interval 1”):

$$P_{\text{interval 1}} = (\text{no. of ripe fruits in the crown + no. of ripe fruits in the net + no. fruits consumed by monkeys})_{\text{count 2}} - (\text{no of ripe fruits in the crown})_{\text{count 1}} + (\text{no. fruits disappeared})_{\text{count 2}}$$

“Disappeared” fruits were detected by comparing (a) the number of ripe and green fruits in the tree crown during one count with (b) the same quantity during the following count plus the number of fruits consumed in between as indicated by peels. In 1999, when nets were used, a negative result of this comparison (a-b) was interpreted as removal of these fruits from the tree crown. In 2000, with no nets mounted below the tree crowns, a “disappeared” fruit could either have been taken away from the tree crown by a frugivore, or could have fallen to the ground and removed there by a ground-living vertebrate.

Thus, fruit counts resulted in a quantitative determination of the number of ripe fruits produced by each tree per interval. For every tree observed, these ripe fruits produced per interval were summed up during the whole observation period (which almost represented the entire fruiting period) to get a **seasonal fruit crop size** of the tree.

To illustrate the amount of fruits available for consumption during a shorter time period, I calculated the standing crop of ripe fruits for an interval between counts. I did this by adding the number of ripe fruits hanging in the tree crowns at one count to the production of ripe fruits of the following interval:

$$\text{standing crop}_{\text{interval1}} = P_{\text{interval 1}} + (\text{no of ripe fruits in the crown})_{\text{count 1}}$$

3.1.5.2 Results

Fruit crop size and its relationship with tree size

The distribution of seasonal fruit crop sizes of individual trees (= the number of ripe fruits produced during a ripening season) is skewed towards smaller numbers in both 1999 and 2000 (Figure 18 a, b). Hence, productivity is not tightly correlated with tree size: the correlation of tree size and number of ripe fruits produced was only weak, though significant in 1999 (Spearman R = 0.374, t(N-2) = 2.85, p = 0.006, n = 52, Figure 19 a) and not significant in 2000 (Spearman R = 0.185, t(N-2) = 1.78, p = 0.08, n = 92, Figure 19 b). However, in 1999 the most productive tree was also one of the biggest trees. Median productivity of the trees was 45 ripe fruits in 1999 (lower quartile: 21.5, upper quartile: 84.0) and 36 ripe fruits in 2000 (lower quartile: 17.0, upper quartile: 64.0).

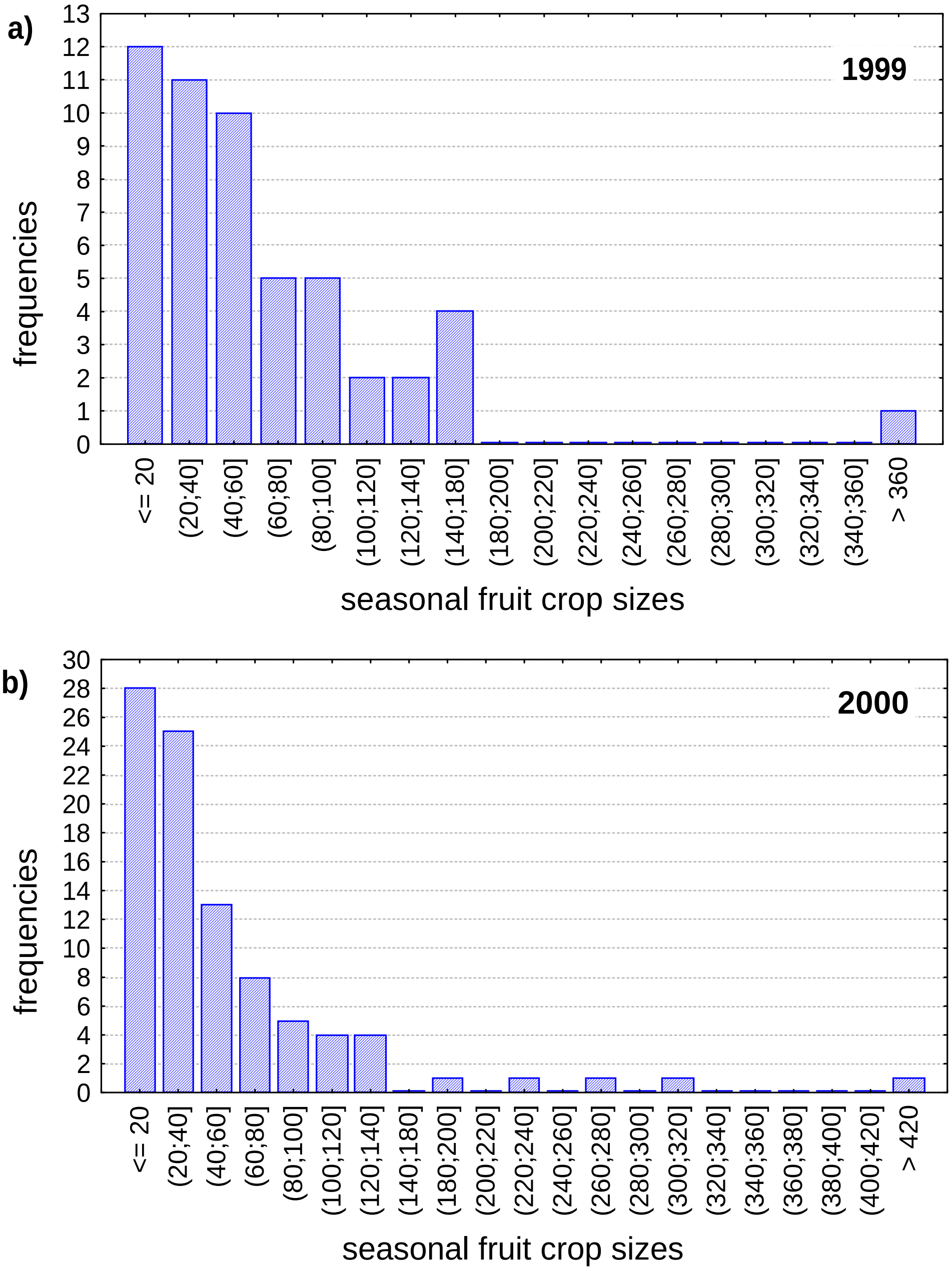

Figure 18: Frequency distributions of productivity of (a) selected trees in 1999 (n=52) and (b) of two local populations in 2000 (n=92).

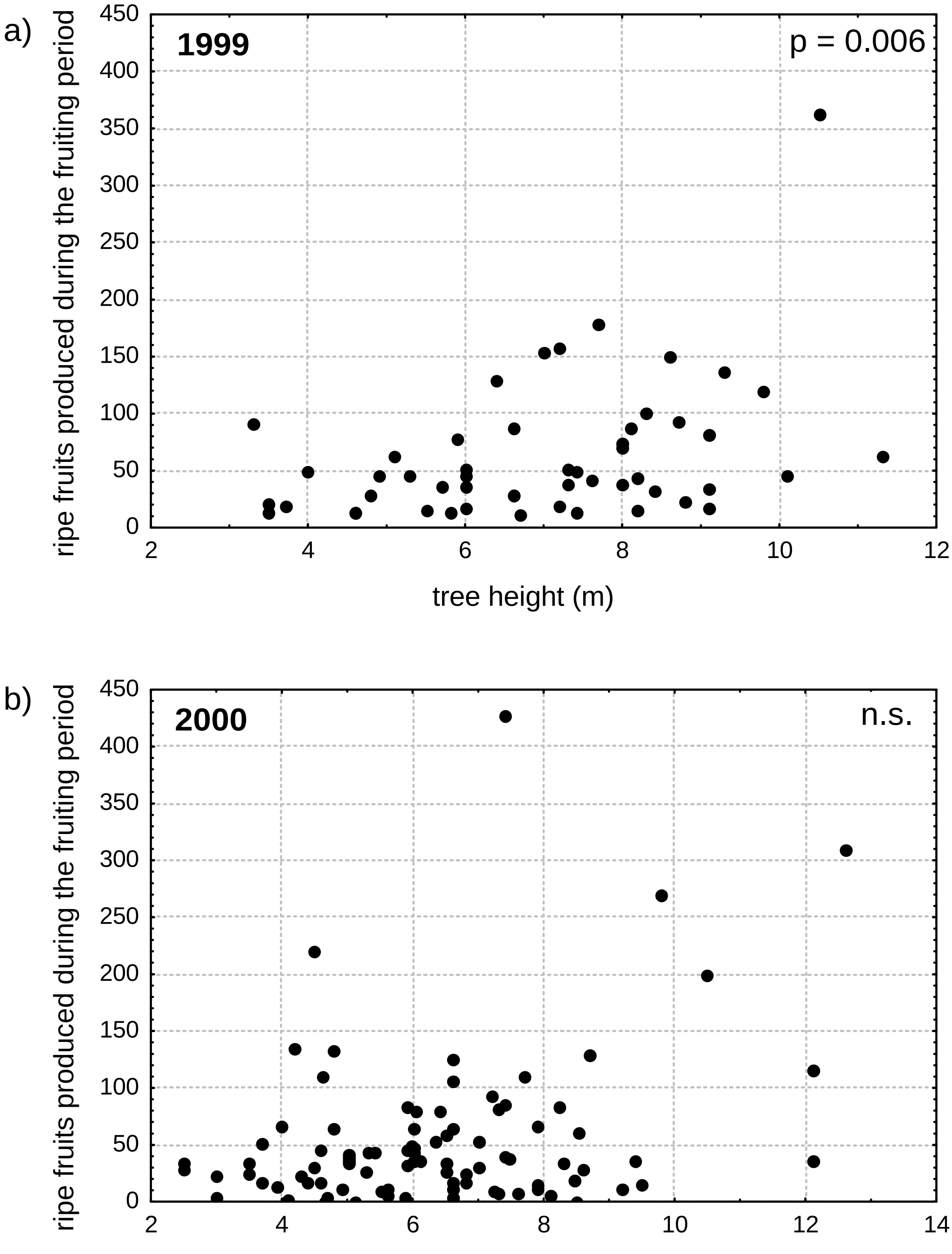

Figure 19: Correlations of total of ripe fruits produced with tree height. Trees monitored (a) 1999 (n = 52), and (b) 2000 (n = 92).

Inter-annual variation of individual fruit production

I found considerable variation in productivity of the individual trees between years (Figure 20). There was no correlation between the total production of ripe fruits of trees during the fruiting period monitored in 1999 and that in 2000 (Spearman R = 0.224; t(N-2) = 1.03; p = 0.32).

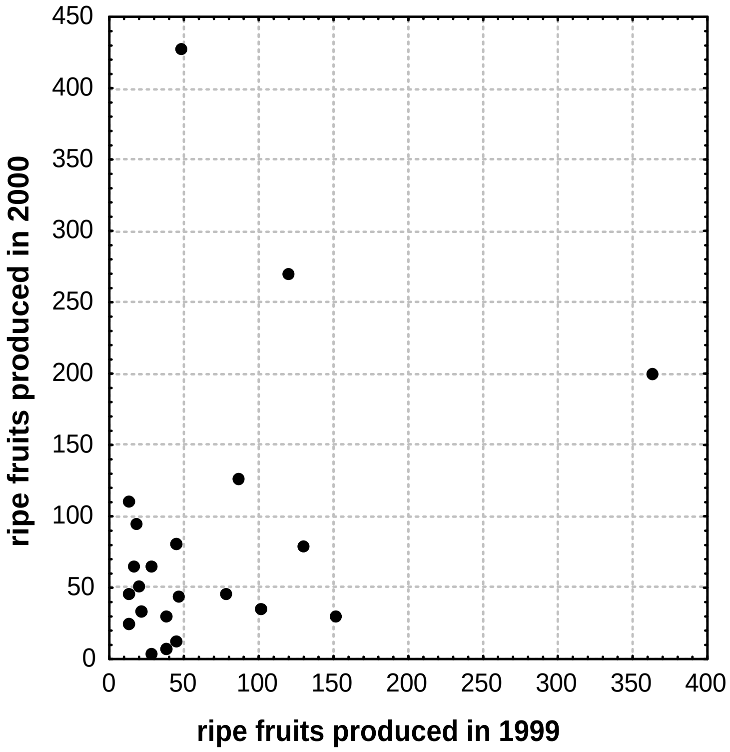

Figure 20: Variation of productivity in successive years - trees with data from both 1999 and 2000 (n = 22).

Standing crop

The standing crop per count interval gives a picture of the amount of ripe fruits available for frugivores in a given tree throughout a shorter time period. In 1999, with count intervals of ca. two weeks, the standing crops of 75% of the trees did not exceed 20 ripe fruits in almost all count intervals (Figure 21 a). Among the 25% trees offering more ripe fruits, the maximum standing crop was 172 ripe fruits. In the fruiting season of 2000, with count intervals of approximately one week, the standing crops of 75% of all trees were low, too, reaching up to 30 ripe fruits (Figure 21 b). The maximum standing crop of a single tree in 2000 was 324 ripe fruits. Large standing crops resulted from accumulation of ripe fruits because of low harvest by frugivores.

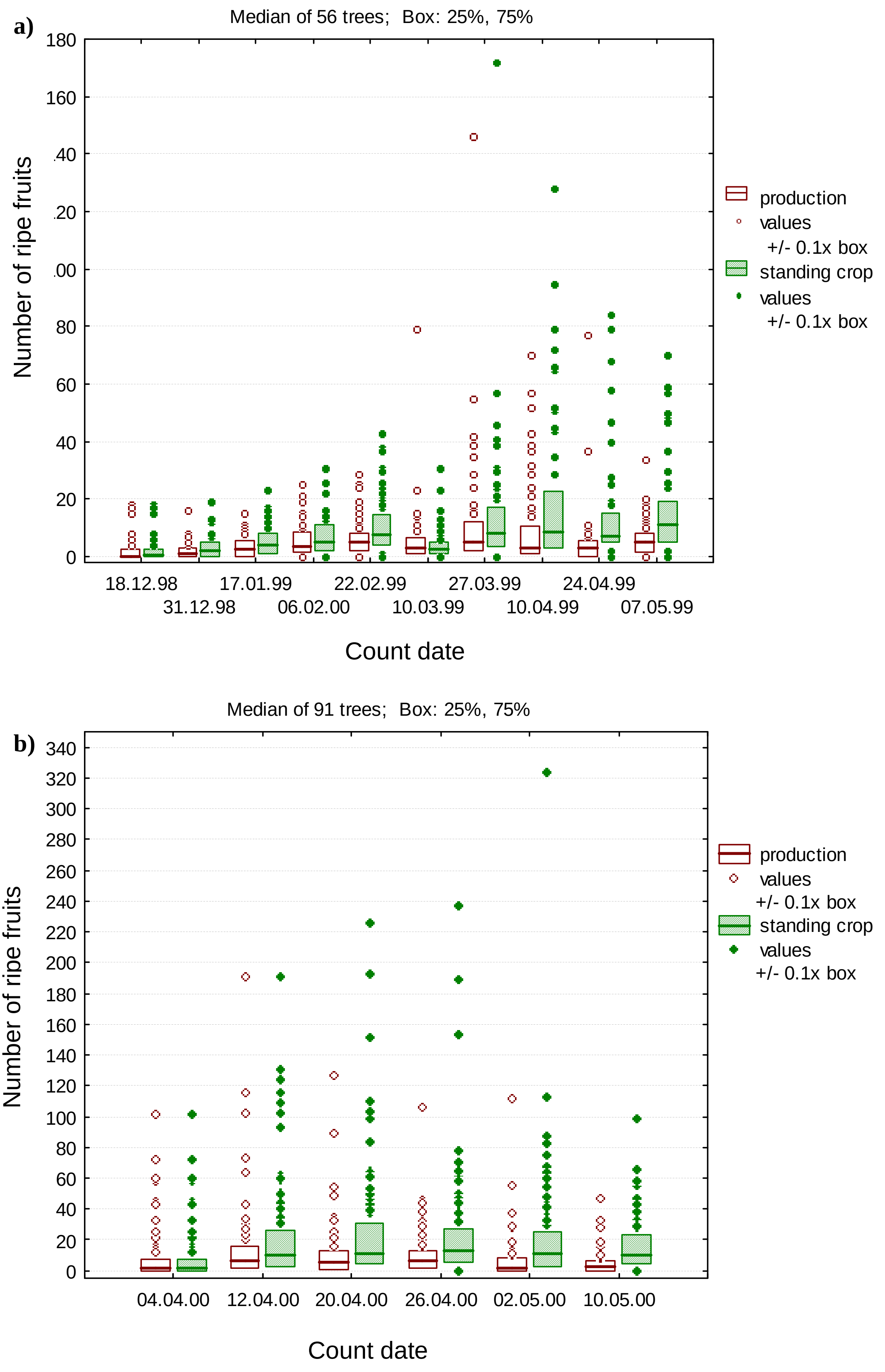

Figure 21: Production of ripe fruits and standing crop of ripe fruits during count intervals in (a) 1999 and (b) 2000.

3.1.6 Infestation of fruits by insect larvae

3.1.6.1 Methods

Fruits fallen into the nets (in 1999) were individually inspected and their state was categorized as intact, perforated peel, rotten, or dry. Fruits with a perforated or somehow otherwise damaged peel were opened and searched for insect larvae. A collection of insect larvae was conserved in ethanol. Also the tree crowns were scanned for signs of insect "pests" during the fruits counts.

Complete fruits infested with insect larvae were taken to the field laboratory and deposited in plastic cages in an attempt to get hold of adult insects emerging from the larvae that fed on the fruits.

3.1.6.1 Results

In 1999 I observed that fruits recollected from the nets had small holes (approx. 0.5 mm in diameter) and in many trees I found lepidopteran webs at the stem base of fruits. Fruits with holes contained always larvae of lepidopterans, most times also dipteran larvae and sometimes also coleopteran larvae. Of the fruits recovered in the nets only fruits with holes were infested with these insect larvae. Lepidopteran larvae were found to feed on the seeds. Infested fruits showed signs of decay already when picked from the tree crown.

Infested fruits were found only between the 8th of January and the 3rd of March 1999, i.e. only in the first half of the observation period. 30% of ripe fruits produced by all focus trees during this part of the fruiting season were infested with insect larvae. Most infested fruits occurred during February. Calculated for the complete fruiting season, 15% of all ripe fruits produced by all focus trees were damaged by insect infestation.

No infested fruits were found during the fruiting season in 2000 and no webs were observed in that year.

3.1.7 Discussion

Size, density, and spatial distribution

The survey of a large number of *L. cymosa*-trees leaves no doubt that this species is truly a small tree of the under-story of the rain forest. This forest layer is very diverse in Cuyabeno where trees with a height of <10 m accounted for 49 % of the tree species richness in a 1 ha plot very close to my study site (Valencia et al. 1994; Valencia et al. 1997). Judging by the size of *L. cymosa* alone, the variety of potential frugivores exploiting it might be limited because the distribution of bird and monkeys species in tropical forests follows a height stratification and few frugivores forage in the under-story that are large enough to deal with *L. cymosa*-fruits (Marra et al. 1997; Buchanan-Smith et al. 2000; Heymann et al. 2002; Schaefer et al. 2002; Walther 2002; Warner 2002).

The size distribution of fertile individuals of *Leonia* in my study site (trees with a diameter of breast height ≥ 2 cm) resembles a normal distribution, with a slightly longer tail of rare, large individuals. This is a size distribution resembling that of shade tolerant canopy trees on Barro Colorado Island (Wright et al. 2003) whereas species dependent on gaps for regeneration showed many large individuals and a long tail of small ones in BCI. For a sub-canopy tree like *L. cymosa*, shade tolerant regeneration would be rather expected. As I observed seedlings in many shaded sites, it is very improbable that *L. cymosa* would depend on directed dispersal to light gap sites for germination and regeneration.

L. cymosa has an aggregated spatial distribution of individuals, a common trait of rainforest trees (compare He et al. 1997; Bleher et al. 2002). Recruitment simulation models of Bleher and Oberrath et al. (Bleher et al. 2002) showed that low to medium dispersal distances always resulted in highly clumped tree populations. It is tempting to conclude that groups of trees of the same size observed at various sites in the study area may be cohorts of related trees and thus a result of low dispersal distance. The data on frugivores visiting *L. cymosa* presented in the following chapter, will allow conclusions on dispersal distances of *L. cymosa*-seeds. However, only genetic data on relatedness of trees would make it possible to find out if tree clusters are descendants of local trees or stem from seeds imported into the area by frugivores.

L. cymosa belongs to the more common trees in Cuyabeno, at least in the forest near the Laguna Grande, where all my study sites were located. Its median density of 12 trees per ha is within the range of 10 to 48 ind./ha reported for the 30 most common trees from the

Cuyabeno hectare plot (Valencia et al. 1994) located at a distance of approximately 1.1 km from the Laguna Grande. No data from other sites are available for further comparisons.

Flowering and fruiting seasons

Following the classification framework of Newstrom and Frankie et al. (1994), *L. cymosa* clearly shows a sub-annual periodicity in reproduction. One flowering event occurs in early March and a second one in October. As a consequence, trees fruit two times a year, and fruit maturation after one flowering frequently overlaps with the subsequent flowering. My data suggest that the forest-wide fruit production of *L. cymosa*-trees resulting from the flowering in October is higher than that resulting from flowering in March, because of the higher percentage of flowering trees in October. Also, fruiting in the following March is less variable in onset and duration than fruiting in August to October.

Like *L. cymosa,* other tree species from tropical forests near the equator also show bimodal flowering (and fruiting) (Borchert et al. 2005, p.629). Obviously, a flowering induction mechanism exists at low latitudes that is not yet well understood. Borchert and Renner et al. (2005) proposed that changes in sunset time (instead of day length like in temperate plants) around the spring and autumn equinoxes function as a signal for flower development. Such a triggering mechanism may work in *L. cymosa*, at least the two flowering seasons per year observed in *L. cymosa* match perfectly with the equinoxes. Also, changes in sunset time are bigger around the autumn equinox than around the spring equinox (7 min / 20 days vs. 5.9 min /20 days, (Borchert et al. 2005, p.629). The weaker photic signal at the spring equinox might account for a lower percentage of *L. cymosa*-trees flowering in spring and subsequently for a less pronounced fruiting period in August. However, the importance of sunset time in flowering induction is not yet experimentally tested. Other, climatic factors might trigger flowering in tropical trees as well, like insolation duration, or draught. For example, Wright et al. (1999) observed on Barro Colorado Island, Panama, that mild, rainy dry seasons (in years after El Nino years) coincide with low or failed fruit production, resulting in famine in frugivores.

It is interesting to note in this context that a bimodal pattern of reproduction in tropical habitats near the equator is also known from birds. In the Lagunas de Cuyabeno, which are located at the Equator, the hoatzin (*Opisthocomus hoazin*) breeds two times a year, while hoatzins in Venezuela (10°N) and in Peru (10°S) breed only once a year (Müllner et al. 2007). The timing of breeding in birds that live at the Equator still remains far from being understood (Hau et al. 2008).

Fruit characteristics

The size and outer woody peel of the fruits of *L. cymosa* are likely to limit the range of frugivores that are able to consume them. Entire fruits could conceivably only be swallowed by large birds with a gap width of 2 cm and more, large monkeys, or at the ground by pacas and deer. If not swallowed entirely, extensive handling is needed to open them. Once having achieved to open the fruit peel, frugivores face a fruit pulp that is sticky and tightly connected to the seeds. Frugivores can only swallow the seeds and fruit pulp together or suck on the seeds and spit them out afterwards. Seed size also makes swallowing difficult or impossible for small birds. For those frugivores that are able to open the peel, relative handling costs do not decrease for bigger fruits because the pulp seed ratio does not increase with fruit size. Therefore I would not expect frugivores to prefer large fruits.

The large size, dull yellow color, relatively strong fruit peel, and no obvious smell (for humans) of ripe fruits of *L. cymosa* are a set of traits characteristic for the "mammal disperser syndrome" (van der Pijl 1982; a summary of "consensus" fruit syndromes in Howe 1986; Fischer et al. 1993). The fact that the fruit pulp of *L. cymosa* is rich in carbohydrates and proteins supports this classification.

My analysis of the nutritional contents of fruits has revealed tree-specific sugar composition and a significant variation of quality of ripe fruits between tree individuals. I paid careful attention to sampling only fruits of similar size and ripeness. Therefore I am confident that the detected differences between trees are real and not an artefact of sampling. This means that a preference of frugivores for individual trees based on nutritional fruit quality is in principle possible. The lack of difference in nutritional quality between recently ripened (green to yellow) fruits and fully ripe (yellow) fruits supports my classification of both stages being "ripe" fruits as far as the nutrients in the fruit pulp are concerned. However, seeds from green to yellow fruits might not yet be ready for germination.

Productivity of individual trees

Small fruit crops are typical of *L. cymosa.* Seasonal fruit crop sizes vary strongly within trees of comparable size and large crops are not restricted to large trees. Also, the variation of seasonal fruit crop size within individuals between two consecutive seasons is large. Variation itself can be expected, but no clear pattern emerged as to what factor might influence the productivity of a tree. There is only a weak correlation between tree size (height) and the production of ripe fruits, and comparing data for individual trees from two main fruiting seasons in 1999 and 2000 did not reveal "prime producers" or "bad producers". There is neither a hint for costs of reproduction: if fruit production was a costly process, one might expect highly productive trees from the first year to produce low numbers of ripe fruits during the following season (i.e. an accumulation of data points in the lower right hand side of the graph in figure 10). Instead, no significant correlation of production of ripe fruits between two consecutive years was found. Variation in fruit production of individual trees could also be the result of varying local ambient conditions, like light, water and nutrient availability. Thus, whatever the reason for inter-annual differences in fruit production might be, individual *L. cymosa* trees are no predictable food resource between fruiting events. Long-lived frugivores might still memorize single trees to be worth a visit, if they have shown to be an attractive fruit resource before.

Traits of *L. cymosa* and the "specialist / generalist" disperser paradigm

Almost all traits of *L. cymosa* described in this chapter – fruit size, seed size, fecundity, and nutrient composition – do indeed meet the criteria listed for a specialized dispersal system (as summarized by Howe 1993). *L. cymosa*-fruits are large and produce large seeds, and its fruit pulp offers proteins additionally to carbohydrates. Median and maximum crop sizes are low. In addition the fruiting season tends to be long. A long fruit display time is hypothesized to yield a better usage of a limited disperser assemblage (Howe et al. 1977). From that perspective, the second fruit set observed in *L. cymosa* could be seen as a strategy to even further extend the time of fruiting and the use of dispersal agents.

In the following chapter I will examine, if frugivores using *L. cymosa* also fit into the proposed specialist dispersal system. The data on life history of *L. cymosa* presented here will provide the basis for hypotheses on plant-frugivore relations to be tested in subsequent chapters.

References

Bleher, B., R. Oberrath and K. Bohning-Gaese (2002). Seed dispersal, breeding system, tree density and the spatial pattern of trees - a simulation approach. Basic and Applied Ecology **3**: 115-123.

Borchert, R., S. S. Renner, Z. Calle, D. Navarrete, A. Tye, L. Gautier, R. Spichiger and P. von Hildebrand (2005). Photoperiodic induction of synchronous flowering near the Equator. Nature **433**: 627-629.

Buchanan-Smith, H. M., S. M. Hardie, C. Caceres and M. J. Prescott (2000). Distribution and forest utilization of Saguinus and other primates of the Pando Department, Northern Bolivia. International Journal of Primatology **21**: 353-379.

Fischer, K. E. and C. A. Chapman (1993). Frugivores and fruit syndromes: differences in patterns at the genus and species level. Oikos **66**: 472-482.

Hallock, Y. F., R. C. Sowder, L. K. Pannell, C. B. Hughes, D. G. Johnson, R. Gulakowski, J. H. Cardellina and M. R. Boyd (2000). Cycloviolins A-D, anti-HIV macrocyclic peptides from *Leonia cymosa*. Journal of Organical Chemistry **65**: 124-128.

Hau, M., N. Perfito and I. T. Moore (2008). Timing of breeding in tropical birds: mechanisms and evolutionary implications. Ornithologia Neotropical: in press.

He, F. L., P. Legendre and J. V. LaFrankie (1997). Distribution patterns of tree species in a Malaysian tropical rain forest. Journal of Vegetation Science **8**: 105-114.

Heymann, E. W., F. Encarnacion and J. E. Canaquin (2002). Primates of the Rio Curaray, northern Peruvian Amazon. International Journal of Primatology **23**: 191-201.

Howe, H. F. (1986). Seed dispersal by fruit-eating birds and mammals. Seed dispersal. D. R. Murray, Academic Press, Australia**:** 123-189.

Howe, H. F. (1993). Specialized and generalized dispersal systems: where does 'the paradigm' stand? Vegetatio **107/108**: 3-13.

Howe, H. F. and G. F. Estabrook (1977). On intraspecific competition for avian dispersers in tropical trees. American Naturalist **111**: 817-832.

Howe, H. F. and J. Smallwood (1982). Ecology of seed dispersal. Ann. Rev. Ecol. Syst. **13**: 201-228.

Marra, P. M. and J. V. Remsen Jr. (1997). Insights into the maintenance of high species diversity in the Neotropics: habitat selection and foraging behavior in understory birds of tropical and temperate forests. Ornithological Monographs **48:** 445-483.

Müllner, A. and K. E. Linsenmair (2007). Nesting behavior and breeding success of Hoatzins. Jounal of Field Ornithology **78**: 352-361.

Newstrom, L. E., G. W. Frankie and H. G. Baker (1994). A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. Biotropica **26**: 141-159.

Schaefer, H. M. and V. Schmidt (2002). Vertical stratification and caloric content of the standing fruit crop in a tropical lowland forest. Biotropica **34**: 244-253.

Valencia, R., H. Balslev and G. Paz y Mino (1994). High tree alpha-diversity in Amazonian Ecuador. Biodiversity and Conservation **3**: 21-28.

Valencia, R., H. Balslev and G. Paz y Mino (1997). Tamaño y distribución vertical de los árboles en una hectárea de un bosque muy diverso de la Amazonía ecuatoriana. Trabajos Ecuatorianos en Botánica. R. Valencia and H. Balslev. Quito, Publicaciones de la Pontificia Universidad Católica del Ecuador.**:** 173-187.

van der Pijl, L. (1982). Principles of dispersal in higher plants.3 rd. Berlin, Springer.

w3TROPICOS (2005). Searched item: *Leonia cymosa* (18.6.2005), Missouri Botanical Garden, St. Louis, Missouri.

Walther, B. A. (2002). Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. Journal für Ornithologie **143**: 64-81.

Warner, M. D. (2002). Assessing habitat utilization by neotropical primates: A new approach. Primates **43**: 59-71.

Wright, S. J., C. Carrasco, O. Calderon and S. Paton (1999). The El Nino Southern Oscillation variable fruit production, and famine in a tropical forest. Ecology **80**: 1632-1647.

Wright, S. J., H. C. Muller-Landau, R. Condit and S. P. Hubbell (2003). Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology **84**: 3174-3185.

3.2 Frugivores of *Leonia cymosa* in the rain forest of Cuyabeno

Abstract

Fruit morphology and fruit color allow predictions as to the type of frugivore species feeding on the fruit. As shown in the previous chapter, fruit traits and ripening regimes of *Leonia cymosa* were in accordance with a “specialist” dispersal system, and with a dispersal of seeds by mammals. Here I investigate which frugivores feed on *L. cymosa* and their role in this tree’s dispersal system. I applied direct observations, automatic camera traps, counts of fruits in tree crowns, and counts of their remains on the floor below the trees.

Black mantle tamarins, *Saguinus nigricollis* (Callitrichidae), and Squirrel monkeys, *Saimiri sciureus* (Cebidae), and possibly an unknown nocturnal frugivore consumed the fruits of *L. cymosa* at my study sites near the Laguna Grande de Cuyabeno, Ecuador. Green-rumped acouchis (*Myoprocta pratti*, Dasyproctidae) consumed fallen fruits and seeds underneath the trees. Black mantle tamarins swallowed the seeds together with the fruit pulp and defecated intact seeds far away from the mother tree. Squirrel monkeys opened the fruits to suck and gnaw on the fruit pulp, and then dropped seeds to the forest floor below the tree crowns. Squirrel monkeys might have carried fruits to neighboring trees occasionally.

55% of all feeding visits recorded in the fruiting season of 2000 were visits by tamarins, and only 45% were visits by squirrel monkeys. Yet, squirrel monkeys in total harvested almost three times more fruits of *L. cymosa* than tamarins, due to their larger group size and other feeding technique. Tamarins visited the study plots more frequently than squirrel monkeys (in one plot e.g. mean interval between harvest of 1.8 days versus 4.3 days), and tamarins fed on fewer trees per visit in a plot than squirrel monkeys (in one plot e.g. mean number of trees exploited per visit of 3.2 versus 7.8). In a single tree, tamarins harvested from 1 to 25 fruits per visit, while squirrel monkeys harvested from 1 to 224 fruits per visit. Both monkey species left ripe fruits behind in the tree crowns in 97% of all feeding events. Both monkey species together consumed 9% of the ripe fruits produced by all trees monitored during the fruiting season of 1999, and roughly 50% of the ripe fruits produced by all trees monitored in the fruiting season of 2000.

Each of my study plots fell into the core home range of one group each of *Saguinus* and *Saimiri*. Thus, the frugivore assemblage is small and disperser availability is limited for the individual tree.

The criteria of a “specialist dispersal system” (Howe 1993) also apply to the frugivore side of the dispersal system of *L. cymosa*. Black mantle tamarins are obviously important dispersers for *L. cymosa*. The interaction between *S. nigricollis* and *L. cymosa* seems close enough to expect a potential for selective influences of the disperser on fruit or fruiting traits.

3.2.1 Introduction

Fruit morphology and color allow predictions as to the type of frugivore species feeding on it. Comparative studies of fruit features and associated disperser assemblages revealed that complexes of fruit characters called “fruit syndromes” (van der Pijl 1969) correspond to a certain group of dispersers (Howe 1986, p.152). For example: small red or black, juicy drupe-like fruits that are rich in carbohydrates are “bird fruits”, while large green, yellow or brown fruits with stronger peels (pericarp) containing lipids or proteins additionally to carbohydrates are often dispersed by primates or bats. Overlap in frugivore consumers exists, especially in unprotected fleshy fruits (Gautier Hion et al. 1985), but fruit syndromes nonetheless give a first hint on the community of frugivores likely involved in seed dispersal of a given plant.

Going beyond van der Pijl’s initial fruit syndrome classification Snow (1971), McKey (1975), and Howe (1982) suggested fruit characteristics together with fruit crop sizes and fruit display features as having evolved in interaction with frugivores to ensure a certain dispersal strategy. These authors postulated two main strategies for tropical trees, one targeting unspecialized frugivorous birds (the generalist dispersal system), and the other targeting bird and mammal species that are highly specialized on a fruit diet (the specialist dispersal system; summarized in Howe (1993)). However, the co-evolutionary history assumed for the latter system requires close interactions between plants and frugivores. An example for such interactions are Neotropical strangler figs, where fig colour, size, smell, and synchrony of ripening are the distinguishing characters that separate bird-dispersed from bat-dispersed strangler fig species (Kalko et al. 1996; Korine et al. 2000). Other case studies on tropical bird-dispersed trees could not find the specialised relationships postulated (Wheelwright et al. 1982) or could not confirm preferences of frugivores for certain fruit traits (Hovestadt 1997).

As shown in chapter 3.1, fruit traits and ripening regimes of *Leonia cymosa* are in accordance with a “specialist” dispersal system, and with a dispersal of seeds by mammals. The Siona indigenous people of Cuyabeno know that some monkeys like *L. cymosa*-fruits: in the Siona language, *Leonia* is called “food of tamarins” (“sisi ëu”) (T. Criollo, personal communication). However, detailed and systematic observations are needed to find out if large frugivorous birds like toucans or fruit crows, or if bats also feed on fruits of *L. cymosa*. Here, I describe the assemblage of fruit users of *L. cymosa* observed in the rainforest near the Laguna Grande de Cuyabeno, Ecuador. I further aim to characterize the nature of the relationship between each of them and *L. cymosa*, taking into consideration their impact on fruit removal, their qualities as dispersers, and the time pattern of fruit removal. Thus I aim to clarify, if any close plant-frugivore interactions exist in this dispersal system.

3.2.2 Visitors of fruiting trees – species and feeding behavior

3.2.2.1 Methods

Observations

To observe frugivores feeding in *L. cymosa*-trees, camouflaged hides were installed on the ground in two patches containing several trees with a good abundance of ripe fruits. From these hides, up to 5 trees could be observed simultaneously, depending on the observation site. A total of 97 hours of observation were conducted between February to April of 1999 and in April 2000. Observation hours were either from 6:15 to 12:00 or 15:00 to17:30, with two thirds of the total observation time being spent in the morning hours. Additionally, careful attention for diurnal frugivores was paid to possible visitors in tree crowns whenever approaching trees for revising fruiting status or for fruit counts.

Only few visits of frugivores could be observed from the hides. Therefore, by following freely moving monkey groups I aimed to collect more information on feeding behavior of black mantle tamarins (*Saguinus nigricollis*) and squirrel monkeys (*Saimiri sciureus*) – two potential dispersers. Monkeys were searched in study plots **HL, J, S**, and **P** during 10 subsequent days in early March 2000. In each area, one observer quietly moved around for the entire day (from 6 a.m. to 5 p.m.). On encountering a group of *Saguinus*, the observer followed the moves of these un-habituated monkeys inconspicuously, avoiding an alarm reaction. Monkey groups of *Saguinus* could be followed for a total of 28 hours. Group size and travel routes of *Saguinus* were recorded. Upon encountering a group of *Saimiri* monkeys, only locations of encounters as well as traveling directions were recorded, because we gave priority to finding and observing *S. nigricollis*. Groups of *S. sciureus* travel fast and we found that observing unhabituated *S. sciureus* from a distance did not yield any useful result concerning the feeding behavior in trees of *L. cymosa*. Following groups of *S. sciureus* would have resulted in leaving the study plots rapidly and missing chances to observe *S. nigricollis*.

Location and group size were also recorded whenever encountering monkeys during fruit counts.

I determined the number of groups of *S. nigricollis* existing at the study sites by help of all records of group size and location of encounter in 1999 and 2000, in combination with the travel routes observed in the groups followed in 2000. I concluded to the existence of a distinct group of *S. nigricollis* from repeated records of the same number of individuals at the same location. Because *S. nigricollis* live in small, stable family groups that inhabit a small home range (Izawa 1978; Emmons 1990), this gives a good estimation of group numbers in an area without coat marking. This census technique has been successfully applied in other studies before (de la Torre 1991; de la Torre et al. 1995).

Camera trapping

To detect possible fruit users during the night, and because visits of diurnal frugivores turned out to be rare events, I used two cameras with automatic trigger mechanisms (Figure 1). The camera devices were based on an Olympus DX Trip XB3 pocket camera that was connected with an infra-red sensitive motion detector and a circuit which secured a time lag of 1 min between photos and thus avoided that too many photos were taken from just one animal remaining for some time within the operating distance of the detector. Camera and circuit were fixed inside a water-proof box made out of a food storing plastic bin where the bottom had been replaced by glass. They were connected by cable to the motion detector and a 12 V dry battery to power the circuit. During field tests, the automatic cameras proved to reliably take photographs of small mammals on the ground as well as of bats hovering in front of a fruit bait. I used camera devices in two ways: firstly, I mounted them on a tripod on the forest floor to take photos of vertebrates feeding on seeds and fallen fruits. Secondly, I tied up the tripod sustaining the camera to trunks near a tree crown of *L. cymosa* to take photos of frugivores feeding from the tree. The time of camera surveillance during the peak fruiting season of 2000 added up to 4 days and nights on the ground at one tree and 21 days and nights in the crowns of two different trees.

Figure 1: Automatic cameras installed near tree crowns or on the ground.

Deposition of entire fruits on the ground

In 1999 entire and only freshly fallen fruits found in the nets below tree crowns were arranged on the ground under the nets, distributed randomly within the area of the crown. All other fruits that had accumulated within the nets during the 7 days between two counts were discarded. At the subsequent control, the remaining fruits on the ground were counted and their status (intact or decomposed) was recorded. Intact fruits were left on the ground together with new fruits transferred from the net while decomposed fruits were removed.

3.2.2.2 Results

Visitors of the tree crown and how they treat fruits and seeds

The only frugivores I observed feeding on fruits of *L. cymosa* during the day were Black mantle tamarins, *Saguinus nigricollis* (Callitrichidae), and Squirrel monkeys, *Saimiri sciureus* (Cebidae) (Figure 2). Their ecological characteristics based on studies conducted in Cuyabeno and elsewhere are given in Table 2. No birds were observed eating fruits of *L. cymosa*, neither during observations of trees nor during visits of trees during fruit counts.

Tamarins could be observed four times wile feeding on *L. cymosa*, once from a hide and three times while following groups. From the hide, a single tamarin was observed separating itself temporarily from its group and entering a tree crown of *L. cymosa* while the other tamarins of the group remained out of sight of the observer and moved on. The single tamarin picked a fruit from a branch, and opened the peel with a bite. The animal used the claws of its fingers to take out single seeds and to put them into its mouth. It also ate the pulp/ seeds directly with the mouth. Seeds were obviously swallowed together with fruit pulp, as no spitting out of seeds could be observed, and because the animal dropped the empty peel on the ground. After consuming two fruits, the individual left the tree crown with a third fruit in its mouth, and followed its group in rapid jumps. Therefore it was impossible to observe how far it carried the fruit and what it did with the fruit later. Many other ripe fruits remained untouched in the tree crown. At all three observations made while following tamarin groups, black mantle tamarins stayed in the tree crowns to feed on a few fruits, and did not carry fruits away from the tree.

The characteristic fragments of fruit peels that tamarins leave behind on the ground below a tree are demonstrated in Figure 3. However, tamarins did not always manage to swallow all seeds of a fruit. On some occasions, we also found small numbers of seeds covered with fruit pulp on the ground beneath peel fragments.

Table 2: Biological facts on *Saguinus* and *Saimiri* (compiled from Ulloa 1988; Emmons 1990; de la Torre 1991; Garber 1993; Peres 1993; de la Torre et al. 1995; Lima et al. 2003)

	Saguinus nigricollis	***Saimiri sciureus***
Weight	400 - 500 g	600 g, males up to 1400 g
Group size	4 - 9 individuals	20 - 50 individuals
Home range size	40 - 50 ha	> 1000 ha
Daily range	1 km	> 2 km
Preferred foraging stratum	3 - 15 m	3 - 25 m
Food	fruits, gums, insects	fruits, 20-80 % animal prey, mostly arthropods

Figure 2: *Saguinus nigricollis* (left) and *Saimiri sciureus* (right)

Figure 3: Peel fragments left by *Saguinus nigricollis*

Squirrel monkeys left remains that differed from those of tamarins. Many separated seeds could be found scattered over the ground together with peel fragments after feeding of *S. sciureus.* Peel fragments were smaller than those left by tamarins. This is because Squirrel monkeys give the fruits a quicker and rougher treatment by biting and tearing the peels into pieces. Seeds found on the ground left by *S. sciureus* showed a rough-textured surface obviously caused by sucking and gnawing on the fruit pulp. The remains of *S. sciureus* differed from those of *S. nigricollis* markedly, whenever *S. sciureus* had consumed a large number of fruits. However, at one control we observed a *S. sciureus* eating 3 of 5 ripe fruits available in a small tree and leaving only larger pieces of fruit peels.

Monkey density in the study area

Monkey sightings and observations in 2000 revealed that each of my study plots fell into the core home range of one group of *Saguinus* and *Saimiri*, respectively. These results are consistent with surveys carried out in the years before this study (1995-1997; Müllner et al. 2001).

We found a *Saguinus*-group with 8 individuals in **P** (6 sightings), one with 7 individuals in **HL** (8 sightings), one with 6 individuals in **J** (7 sightings), and one with 9 individuals in **S** (1 sighting) (Figure 4). Because home range overlaps exist in tamarins, other groups could have infrequently intruded into home ranges of the mentioned groups. This could explain rare sightings of smaller groups of *Saguinus* in the area. However, these small groups could also be the result of temporary group fission.

Because of the large home ranges of *Saimiri*, it was more difficult to determine the exact number of groups of this species present in the area. One group of *Saimiri* was observed repeatedly to patrol the areas **J** and **HL** and was probably also ranging through the part of **S**, whereas squirrel monkeys sighted in **P** probably belonged to another group (Figure 4).

Visitors at the ground

Fruits deposited on the ground during the fruiting season in 1999 either were removed by unknown animals or decayed. In 2000, photographs taken by the automatic cameras showed that fruits and seeds of *L. cymosa* on the ground attracted acouchis (*Myoprocta pratti*). No other ground mammals triggered the camera traps.

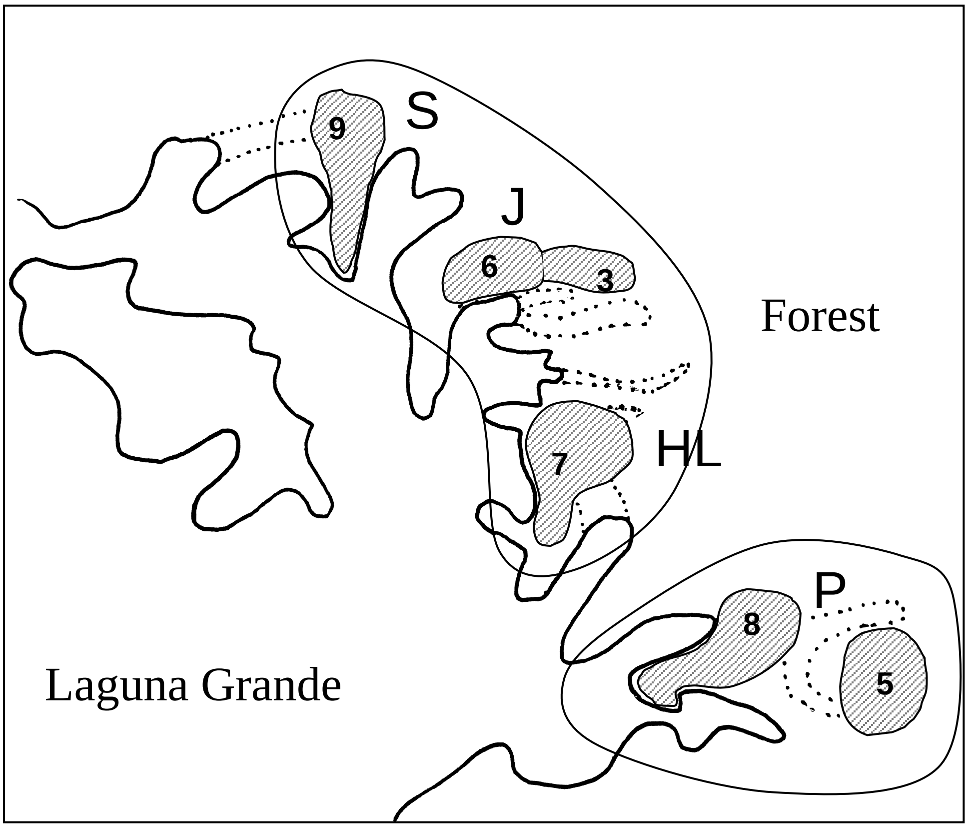

Figure 4: Groups of black mantle tamarins (*Saguinus nigricollis)* and of squirrel monkeys (*Samiri sciureus)* observed at the study sites. Areas of sightings of *S. nigricollis* are hatched, numbers indicate group size. S, J, HL, P: study plots. Tamarin groups falling into the range of one group of squirrel monkeys are grouped by a thin ellipsoid line.

3.2.3 Contribution of frugivores to fruit removal and patterns of use of *L. cymosa* by monkeys

3.2.3.1 Methods

Measuring fruit production and fruit removal

The number of ripe fruits produced by an individual tree, the number of fruits removed from its crown by frugivores, and the standing crop of ripe fruits were determined by means of fruit counts as described in detail in chapter 3.1. Fruit counts in 1999 were conducted biweekly on a sample of 61 *L. cymosa*-trees from study plots **HL**, **J**, **P**, and **S**. In 2000 fruit counts were conducted weekly on all trees carrying fruits in **HL** and **P**, equaling 93 trees of *L. cymosa*. Additionally, I checked all trees in **HL** daily for signs of fruit harvest from 12th of April to 10th of May 2000, and I conducted daily controls of all trees in **P** from 4th to 15th of April and from 17th of April to 10th of May. When peels were found, the number of consumed fruits, and the ripe fruits remaining in the tree crown were counted. Thus, during this period of the fruiting season of 2000 I was able to determine if monkeys visited my study plots with a resolution of one day. A visit of a monkey group to a study plot here means that I found at least one *L. cymosa*-tree with feeding remains of monkeys at a given day.

I express the general contribution of a particular frugivore species to fruit removal in *L. cymosa* by the percentage of fruits removed by this species from the pooled production of ripe fruits by all trees observed throughout the whole fruiting season.

Likewise, I calculated the overall percentage of fruits removed from the ground by using the sum of all fruits manually deposited and the sum of all fruits that disappeared throughout the observation time.

For the purpose of describing the time pattern of overall fruit maturation and fruit removal by monkeys, I pooled the count results of all trees monitored for each count interval.

Assigning fruit consumption to monkey species in 2000

Using the different traces of feeding left by each of the two monkey species, and taking into consideration sightings of monkey groups shortly before tree controls, 93% of the feeding events could be assigned to each species without direct observation. We had difficulties in unequivocally assigning 14 feeding events, with a total of 56 fruits consumed (= 2% of all fruits removed by monkeys). These difficulties arose from finding peel fragments of only intermediate size and/or finding seeds where it was not clear if they had been sucked upon or not.

In these cases I assigned the fruits removed from a tree to *S. sciureus* if the tree belonged to a patch of *L. cymosa*-trees where *S. sciureus* had removed large amounts of fruits. This is reasonable because groups of *S. sciureus* usually contain of 20-40 animals (own observations; Ulloa 1988; Kinzey 1997) and usually spread a whole patch of trees while traveling and feeding. I assigned the fruits removed from a tree with ambiguous feeding remains to *S. nigricollis* if there were no traces of a visit of *S. sciureus* in the plot at that day, and also if such a tree stood more than 30 m away from a patch of trees with feeding traces of *S. sciureus.* ArcView-maps for each control day that visualized the records of fruit consumption were a helpful tool for analyzing the spatial pattern of feeding events.

It is possible that some of the feeding events mentioned were wrongly assigned to *S. sciureus.* Another source of error in assigning feeding events could be that in single cases peel remains indicating fruit removal by *S. nigricollis* might have been overlooked where *S. sciureus* had fed on numerous fruits (e.g. 50 fruits and more in a single tree), and had left large amounts of peel fragments and seeds on the ground.

3.2.3.2 Results

Impact of monkeys

The amount of fruits harvested by monkeys (and in general) differed strongly between the two fruiting periods observed. In 1999 almost two thirds of the total production of ripe fruits of all trees monitored fell unused into the nets (Figure 5 a), 23% of them showing infestation by insect larvae (compare section 3.1.6). Only 9 % of the ripe fruits were harvested by monkeys and three times as many fruits “disappeared”, meaning that they did not remain in the crown, but peels did not appear in the nets. I recorded harvest by monkeys 51 times and events of disappeared fruits 160 times. We searched in a circumference of approximately 5 m of the outer borders of the tree crowns for fruit remains and did not find any.

In 2000, when no nets were used and fruit ripening started two months later, half of the ripe fruits produced population-wide were consumed by monkeys, and almost a third of the fruits “disappeared” by the end of the observation period (Figure 5 b).

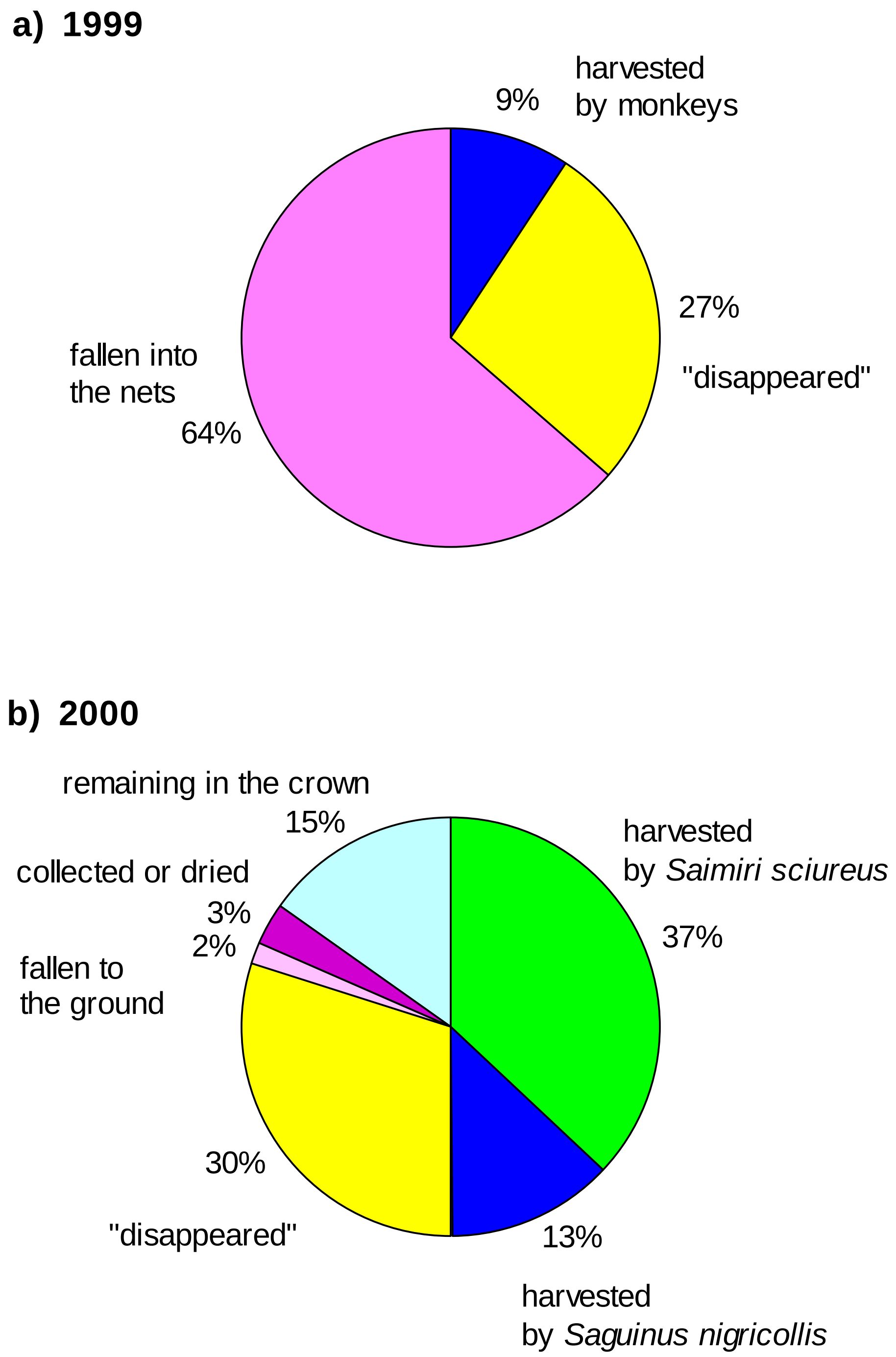

Figure 5: Fate of ripe fruits during the observation periods of (a) 1999 and (b) 2000 in percent of total seasonal fruit production of all trees pooled.

Less than 5% of the fruits were either found lying on the ground or found shrunk by desiccation within the tree crown and thus were not attractive anymore to frugivores. A total of 205 visits of monkeys were recorded in 2000, combining results for all trees. The “disappearance” of fruits was noted in 259 controls of single trees, i.e. also independently of harvests by monkeys documented by peel remains. It has to be pointed out that in 2000 “disappeared” fruits could have either been removed directly from the crown or could have been fallen to the ground and removed by terrestrial animals, whereas in 1999 fruits “disappeared” must have been removed from the tree crown or from a net. The surveillance of tree crowns by automatic cameras did neither reveal any nocturnal frugivores, nor any additional diurnal frugivores. At one occasion I detected by counts that fruits disappeared from the crown of a tree surveyed by a camera without any photograph being triggered off (tree # p69, 02.05.00).

Due to their larger group sizes and their faster and rougher feeding technique, *S. sciureus* consumed more fruits per tree visit than *S. nigricollis*. Squirrel monkeys in total harvested almost three times more fruits of *L. cymosa* than tamarins. On the other hand, 55% of all feeding visits recorded in the fruiting season of 2000 were visits by *Saguinus*, and only 45% were visits by *Saimiri*.

Impact of ground animals

A third of the fruits taken from the nets and placed on the forest floor were removed (Figure 6). Unremoved entire fruits decomposed completely within one to two weeks. As a consequence, seeds remaining inside the fruit peel have no chance to germinate. Green-rumped acouchis (*Myoprocta pratti*, Dasyproctidae) triggered automatic cameras while handling seeds of *L. cymosa* and were often encountered in the forest.

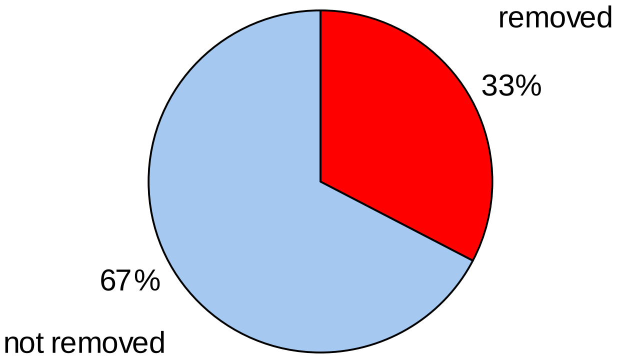

Figure 6: Percent of fruits removed of fruits collected in the nets and then laid on the ground underneath the nets.

Patterns of use of *L. cymosa* by monkeys in April to May 2000

- Time between visits in the plot and number of trees harvested

During the 4 weeks of daily controls in **HL**, *S. nigricollis* consumed fruits of *L. cymosa* on 16 days, with a mean interval between harvest in the plot of 1.8 days (min: 1 day, max: 5 days, cv = 0.73, n=15). The mean number of trees exploited per visit in the plot was 2 trees (min: 1, max: 5, cv = 0.61) During the 5 weeks of daily controls in **P**, *S. nigricollis* harvested fruits of *L. cymosa* on 24 days, with a mean interval between harvest in the plot of 1.5 days (min: 1 day, max: 4 days, cv = 0.6, n=23). In **P**, the mean number of trees exploited per visit was 3.2 (min: 1, max: 13, cv = 0.87).

S. sciureus, on the other hand, consumed *L. cymosa*-fruits in **HL** on 6 days, with a mean time interval between fruit harvest in the plot of 4.3 days (min: 1 day, max: 13 days, cv = 0.71), and exploited a mean of 6.7 trees per day (min: 1, max: 13, cv = 0.97). In **P**, *S. sciureus* harvested fruits on 5 days, and the mean time interval between fruit harvest was 5.7 days (min: 2 days, max: 14 days, cv = 0.75). In this plot, *S. sciureus* harvested a mean of 7.8 trees per day (min: 1, max: 15, cv = 0.66).

- Number of fruits harvested per visit

In a single tree, *S. nigricollis* harvested from 1 to 25 fruits, while *S. sciureus* harvested from 1 to 224 fruits (means are not meaningful in this context because the number of fruits available in the trees under control varied largely). The maximum values represent differences of removal capacity between the two monkey species due to differences in fruit /seed treatment and group size (see above).

Both monkey species left over ripe fruits in the tree crowns in 97% of all feeding events, in large standing crops as well as in small standing crops. I recorded only 7 feeding events with complete harvest of all ripe fruit in a tree, 4 by *S. nigricollis* and 3 by *S. sciureus.* Depletion of ripe fruits during one single feeding visit occurred only in trees with standing crops of up to 20 ripe fruits.

Time pattern of fruit production and fruit harvest throughout the fruiting season

- Results from 1999

In 1998/1999 *L. cymosa*-trees began to produce ripe fruits at the end of December 98. Until the beginning of March almost half of the total number of ripe fruits produced in this fruiting period had already matured. However, almost no fruits were harvested by monkeys until the beginning of March 1999 (Figure 7). Thereafter an abrupt increase of the number of fruits removed by monkeys (*S. nigricollis* and *S. sciureus*) and of the number of trees visited by monkeys occurred. At the onset of this peak, fruit production increased 109% and standing crop increased 48%. Thus the peak of harvest coincided with a marked increase in fruit production and fruit offer.

Fruit removal by “unknown frugivores” was also low in the first three months of the fruit maturation period of 1999 and had its peak at the end of this period. In total, more fruits were removed by unknown frugivores than by monkeys.

- Results from 2000

The period of fruit maturation in 2000 was shorter than that in 1999. In January 2000 none of the observed trees of *L. cymosa* carried ripe fruits. At 22nd of March 00 I counted only 97 ripe fruits in all 92 trees with fruits in plot **HL** and **P**. That amount of ripe fruits was already reached in December ‘98 by only 53 trees.

In 2000, fruit harvest of *S. nigricollis* could be distinguished from fruit harvest of *S. sciureus*. Results are presented separately for **HL** and **P**, because different tamarin groups inhabited these two plots:

a) Plot **HL**

At the third count date the cumulative number of ripe fruits that matured in plot **HL** exceeded half of the total number of ripe fruits matured in this area during the whole fruiting period (Figure 8 a). Fruit production in the second count interval remained almost the same as in the first count interval, yet standing fruit crop rose 69%.

The number of ripe fruits removed by *S. nigricollis* remained at a low level for the first two count intervals, despite of the marked increase of standing crop during the second count interval (12th to 20th of April 2000). Fruit removal by *S. nigricollis* then rose 100% in the

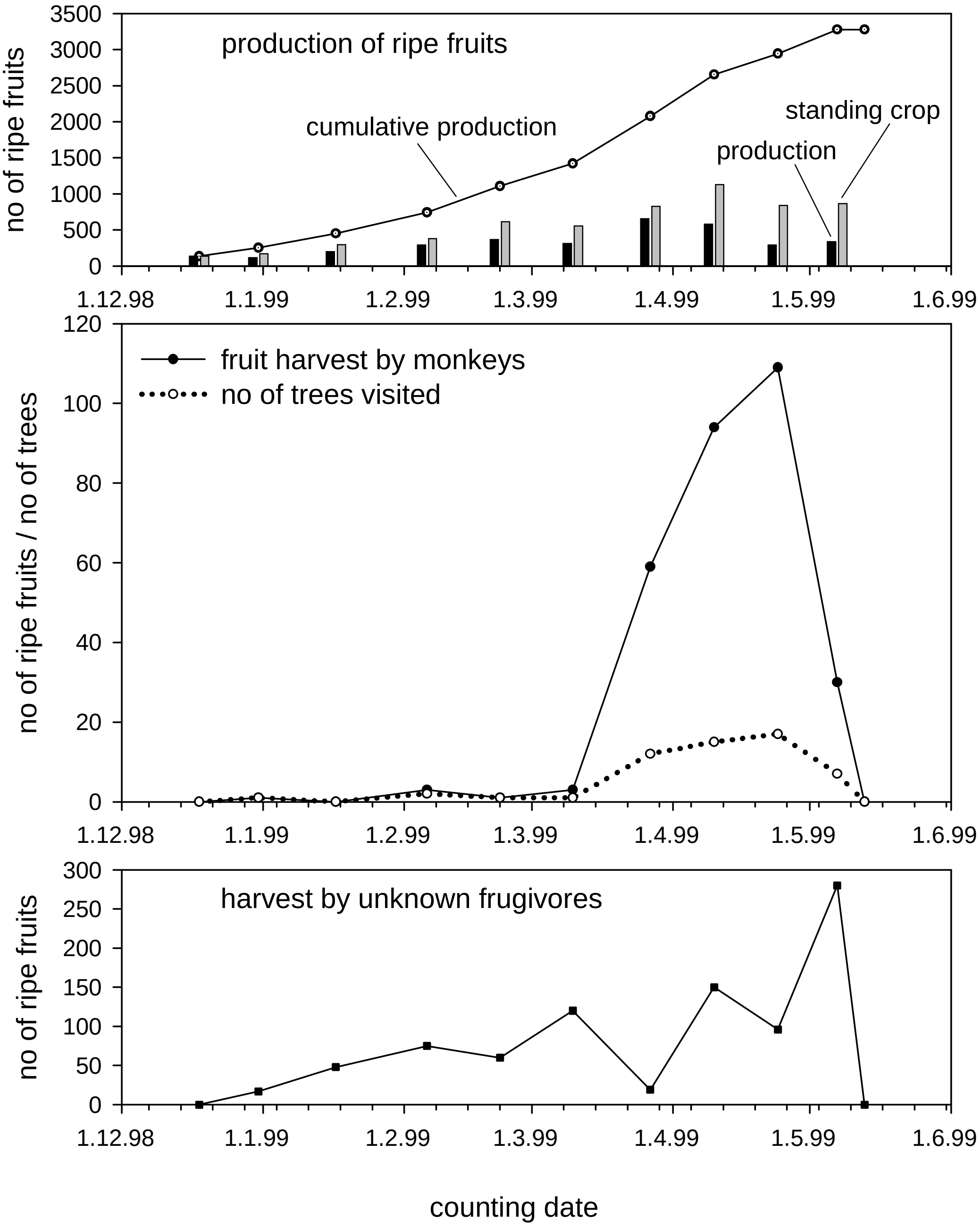

Figure 7: Time pattern of overall fruit maturation and fruit harvest by monkeys and unknown frugivores in 52 trees of *L. cymosa* during the fruiting season from December 1998 to May 1999. Note that all values refer to the interval before, and not to the single count date, except for the first count date.

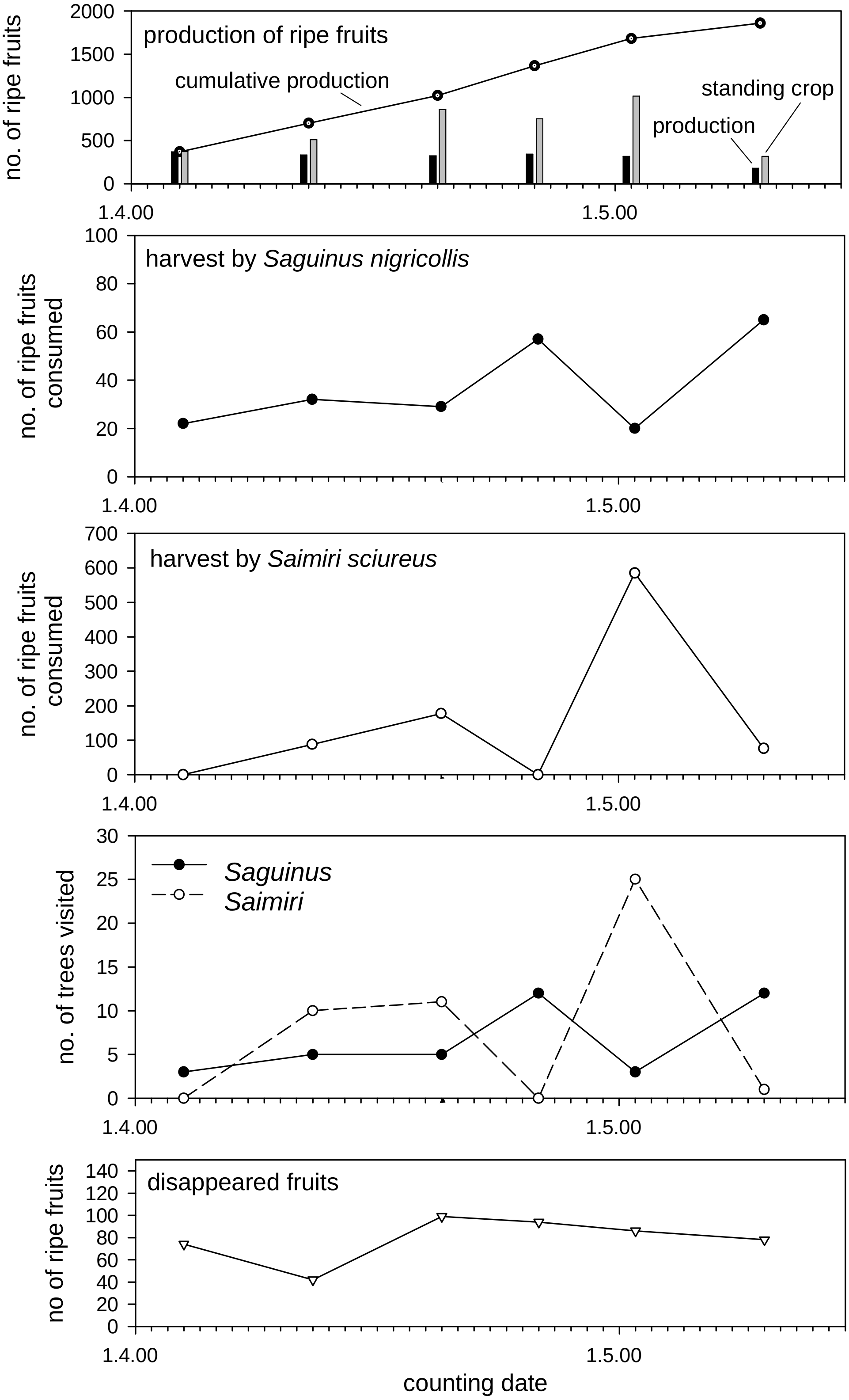

Figure 8 a: Time pattern of fruit maturation, fruit harvest by monkeys, number of trees visited by monkeys, and number of disappeared fruits in the plot **HL** during the fruiting season from April to May 2000. Data are combined from 35 trees of *L. cymosa*. Note that all values refer to the interval before, and not to the single count date, except for the first count date.

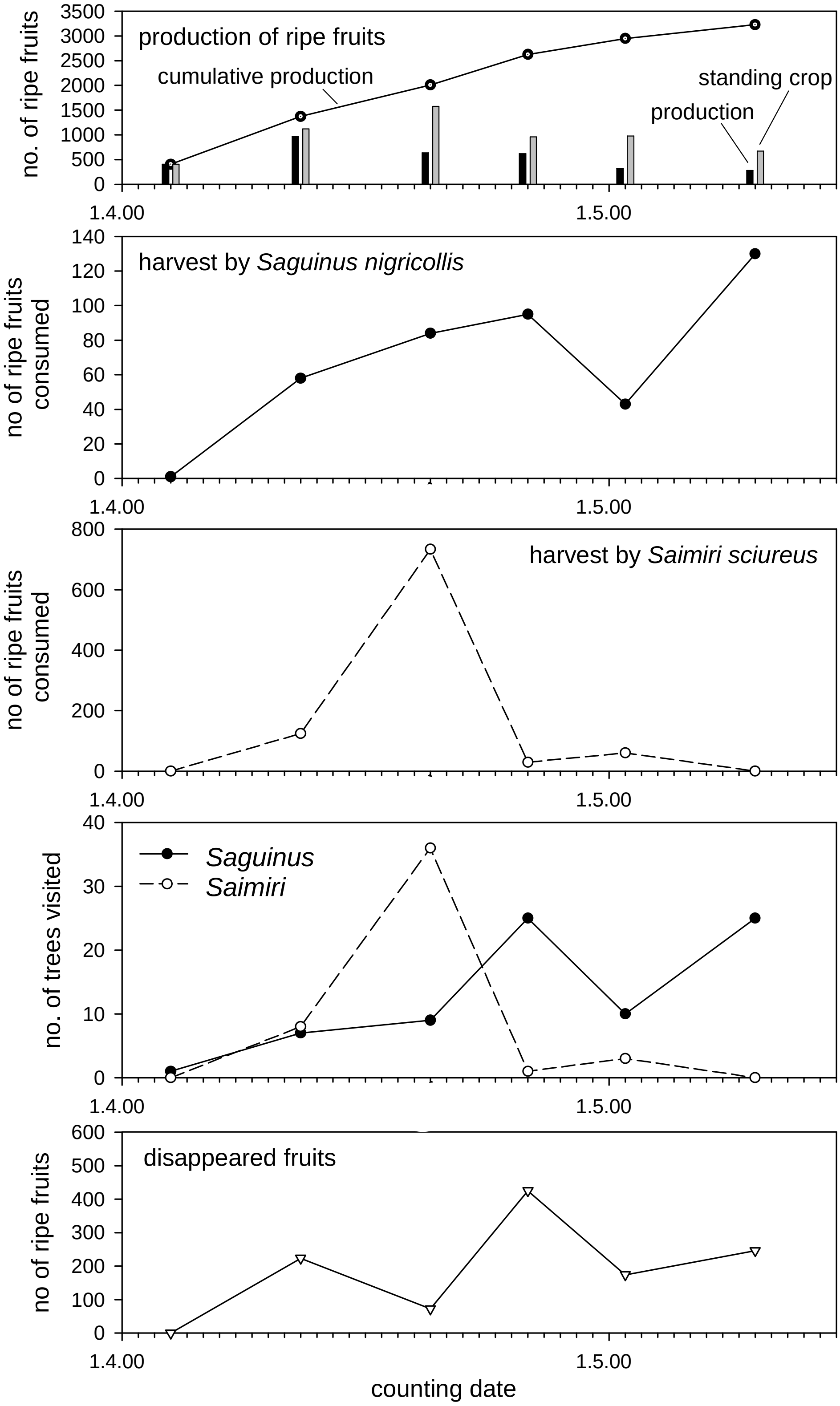

Figure 8 b: Time pattern of fruit maturation, fruit harvest by monkeys, number of trees visited by monkeys, and number of disappeared fruits in the plot **P** during the fruiting season from April to May 2000. Data are combined from 49 trees of *L. cymosa*. Note that all values refer to the interval before, and not to the single count date, except for the first count date.

third interval. In the following, it fluctuated strongly. The group of *S. nigricollis* foraging in **HL** consumed a relatively constant number of fruits per tree visit, as can be noted by the parallel curve progressions of both parameters. The maximum number of trees visited between two counts was 12 (within an interval of 6 days).

Fruit harvest by *S. sciureus* increased steadily at the beginning (note different axis scales of graphs in Figure 8 a) and showed a pronounced peak of fruit consumption at the end of this fruiting period. In between *S. sciureus* had not foraged in the plot for 10 days, resulting in the value of 0 fruits consumed during the third count interval. After this period of absence from the plot, *S. sciureus* visited 25 trees and consumed at total of roughly 600 fruits (within an interval of 6 days). This maximum of fruit consumption activity of *S. sciureus* coincided with the maximum standing crop of fruits per interval.

The quantity of fruits "disappeared" (= fallen to the ground and removed there, or removed from the crown) was relatively constant throughout the fruiting period in this plot during 2000.

b) Plot **P**

In plot **P,** the standing crop of ripe fruits increased strongly already in the first count intervals and peaked in the second count interval. At the end of this interval also the cumulative number of fruits matured in the plot exceeded half of the total number of ripe fruits produced in this plot throughout the entire season (Figure 8 b). The production of ripe fruits showed its peak in the first count interval, that is one before the peak of standing crop of ripe fruits was reached.

Unlike in **HL** the number of fruits harvested by *S. nigricollis* rose steadily in **P**, interrupted only by a drop in number at the fourth count interval. The number of ripe fruits consumed by *S. nigricollis* was not closely linked to the number of trees visited in **P**. For example, tamarins harvested roughly the same amount of fruit in the second and third interval, but visited only nine trees in the first versus 25 trees in the second interval. The latter number of trees was the maximum number of trees visited by *S. nigricollis* between subsequent counts in this plot (within an interval of 6 days). It has to be noted in this context that in **P** also the number of fruiting *L. cymosa* -trees was higher than in **HL**.

The number of fruits harvested by *S. sciureus* showed a single steep peak that coincided with the peak of standing crop in **P**. Strictly parallel to this, the number of trees visited by *S. sciureus* also peaked at the same count date. This pattern of pronounced and parallel peaks of fruit consumption as well as of the number of trees visited by *S. sciureus* was similar to the pattern in **HL**. The maximum number of trees visited by *S. sciureus* between two subsequent counts in **P** was 36 (within an interval of 8 days).

The number of fruits "disappeared" was much more unsteady in **P** than in **HL** and showed a marked peak in the third count interval.

3.2.4 Discussion

Fruit user assemblage

The assemblage of fruit users of *L. cymosa* is small, consisting of *Saguinus nigricollis, Saimiri sciureus,* probably an unknown nocturnal frugivore, and agouchis that use fallen fruits underneath the trees. No birds were observed to harvest these fruits. The small number of diurnal species seems to result from a combination of fruit traits, such as considerable size and protection by a tough peel, and tree height. Tree height can determine the disperser assemblage of a tree in tropical forests, because the vertical space is rather strictly partitioned between species (Peres 1993; Walther 2002). With a mean height of 6.6 m *L. cymosa* displays fruits in a forest layer that is mainly used by *S. nigricollis*and *S. sciureus* out of the 11 monkey species present (Ulloa 1988). Additionally, very few large frugivorous birds forage at that height. I observed toucans and araçaris from the genera *Rhamphastos* and *Pteroglossus* frequently in the canopy near my study plots, but never at low forest strata, and no toucan ever came close to the trees observed directly for many hours. This finding is confirmed by a study in Venezuela, where Schaefer (2002) found toucans preferring tree heights of 8-16 m. In Venezuela only *R. culminatus* also used lower strata additionally. Unless these birds are extraordinarily skilled in the early detection of approaching humans, and move to the canopy at the slightest disturbance, toucans very likely do not play an important role in the dispersal of *L. cymosa*. I also never heard calls that would have indicated the presence of birds capable of eating *L. cymosa*-fruits. I conclude from all this that birds do not disperse *L. cymosa* and are most likely not responsible for the removal of fruits from tree crowns that was not attributable to monkey harvesting activity.

Fruits that disappeared from tree crowns without hints on who had taken them might in part have been carried away by monkeys. This is suggested by the fact that in 1999 fruit removal by unknown frugivores peaked during the period of fruit removal by monkeys (see Figure 7). I observed *S. nigricollis* once to carry entire fruits away, despite the fact that tamarins usually process the fruits they eat directly in a tree crown (C. Knogge, personal communication). The situation in which individuals of *S. nigricollis* carry off fruits in order to keep in contact with the rest of the group might occur more often than observed. Carrying off fruits might also be a behavior of squirrel monkeys, when fighting and chasing each other in competition for food in a fruiting tree. However, if this had occurred frequently, the number of fruits disappeared should have risen to a maximum at the date of peak fruit removal by squirrel monkeys, which it did not. Furthermore, in both study years disappearance of fruits from tree crowns was more frequently recorded than feeding visits of monkeys. This shows that other, possibly nocturnal fruit users of *L. cymosa* may exist. The camera traps used in this study might not have recorded such nocturnal frugivores. This may be concluded from the single record of fruits disappearing from a tree crown surveyed by a camera without any photograph being triggered off. The reason why the camera did not take photographs at this occasion remains unclear to me. Cameras had been tested previous to installation, and showed to be able to take pictures of bats flying in front of a banana bait. Yet, the heat signal of bats hovering in a tree crown might not have been strong enough to trigger a shot, and bats might indeed feed on *L. cymosa*. Cameras should nonetheless have reliably captured larger nocturnal frugivorous mammals potentially feeding on *L. cymosa*, like kinkajous (*Potos flavus)*, and night monkeys (*Aotus spp.*) (Emmons 1990). These should also have left traces of feeding activity. Therefore I conclude that they do not feed on *L. cymosa* in Cuyabeno. If bats were the nocturnal frugivores that ate the fruits registered as “disappeared”, this would imply a remarkable sensory capacity. Fruits taken by bats often emit a scent and/or grow in an exposed manner giving easy access to bats and allowing clutter-free echolocation (Kalko et al. 1998). Some frugivorous leaf-nose bats use olfactory cues for the long-distance detection of ripe fruits and switch to an echo-oriented final localization of the position of the fruit (Thies et al. 1998). However, fruits of *L. cymosa* are scentless and grow in between leafs (see Figure 7 in chapter 3.1). These features are contrary to the idea that bats might feed on *L. cymosa*-fruits. The most helpful tool to find out if bats belong to the frugivores visiting *L. cymosa* would be infra-red video cameras.

Fruits and seeds of *L. cymosa* falling to the ground attract acouchis (*Myoprocta pratti*), as shown by photographs taken by the automatic cameras. I have no indications that other ground mammals use the fruits, but some may do so occasionally, like brocket deers *Mazama americana* and *Mazama guoazumbira* (Emmons 1990).

Effectiveness of fruit consumers in dispersing seeds of *L. cymosa*

Among the two monkey species found to feed on fruits of *L. cymosa* an interesting dichotomy emerged. Tamarins, on the one hand, visited the trees frequently and harvested few fruits per visit. They swallowed entire seeds and thereby dispersed seeds over long distances. In Peru, *Saguinus fuscicollis* was observed to defecate seeds of *L. cymosa* 86-300 m away from the tree where it had consumed the fruits (Knogge 1999). Seeds also were unimpaired by the gut passage and geminated. Tamarins may defecate seeds disproportionately often at sleeping and roosting sites, like it was observed for seeds of *Parkia* (Feldmann 2000). Yet, even this deposition pattern will result in a much lower density of dispersed seeds than of seeds remaining under mother trees. Therefore, it is unlikely that negative secondary density effects after dispersal by tamarins occur. Thus, *S. nigricollis* can be considered reliable dispersers sensu Howe and Eastabrook (1977), because they swallow seeds and deposit seeds in a relatively spread out manner throughout the forest.

S. sciureus, on the other hand, visited the trees in longer intervals and was able to harvest large amounts of fruits per visit of fruiting *L. cymosa*-trees. *S. sciuereus* was the most important frugivore in terms of the total number of fruits removed throughout the fruiting season 2000. However, *S. sciureus*, for most of the time, was not dispersing seeds due to its habit of spitting out seeds while sitting in the tree after having sucked the fruit pulp. At the most some seeds were dispersed at short range, when individual squirrel monkeys took fruits with them in order not to be attacked by other animals from the group. Consequently, *S. sciureus* is not an effective disperser. However, it is not a seed predator either, because seeds that fall to the ground below the tree crown after treatment by *S. sciureus* are intact. Seeds of *L. cymosa* do not need to be digested to germinate. The treatment *S. sciureus* gives to the fruits of *L .cymosa* could be called “unpacking” seeds. By this activity *S. sciureus* saves seeds from decomposition, because entire fruits remaining untreated on the forest floor will rot. However, most of the seeds are removed by acouchies (*Myoprocta pratti*), the only animals that triggered the automatic cameras. As seeds of *L. cymosa* are lightweight they are in all probability not hoarded, but eaten directly (Hammond 1995; Forget et al. 1998). Thus, “unpacking” of seeds by *S. sciureus* neither promotes seed dispersal, nor secondary seed dispersal.

Acouchis should as well eat entire fruits fallen to the ground below *L. cymosa*-trees. I can not rule out that they might also cache some entire fruits. However, I would expect buried fruits to decompose rapidly, including the seeds enclosed, like many fruits I experimentally deposited on the ground. Therefore, I do not believe that acouchies contribute to dispersal of *L. cymosa*. Neither do Brocket deer (*Mazama* sp.) – another potential fruit users on the ground – because as ruminants they chew and destroy seeds during digestion (Forget et al. 1998).

If bats did remove entire fruits of *L. cymosa* and were responsible for the "disappeared fruits", they would rank in degree of fruit removal between *Saimiri* and *Saguinus*. Bats can be reliable seed dispersers, as long as they either swallow seeds or deposit intact seeds evenly at a large number of feeding roosts as has been shown for flying foxes and *Cola cordifolia* (Ebigbo 2004). Without knowing species and feeding habits, I can not further discuss the quality of this potential dispersal agent.

The fate of ripe fruits was markedly different in the two seasons covered by this study. Monkeys removed only about 10% of the fruits from the tree sample in 1999 as opposed to 50% in 2000. I have no indication for differences of the general fruit production in my study area between 1999 and 2000 that would allow interpreting the lower removal of *L. cymosa*-fruits in 1999 in the light of potential competition with other fruit offers. It is, however, possible, that *L. cymosa* ranked lower as a food resource for *S. nigricollis* and/or *S. sciureus* in 1999 than in 2000. It is not unlikely that monkeys might have been deterred by the nets used in 1999 for collecting falling fruits. However, monkeys had a long time to get accustomed to the nets, because these had been installed already two months before the high ripening season. Therefore it is less probable that the nets were the cause of a lower fruit removal by monkeys in 1999. The lower fruit removal can in part be explained by a pest of insect larvae that occurred during the first half of the fruiting season of 1999, while no such infestation of fruits was observed in 2000. Insect infestation caused many fruits to be discharged before they could have been eaten by frugivores.

Time patterns of use of *L. cymosa* by monkeys

The patterns of visits of *S. nigricollis* and *S. sciureus* in my study plots and their harvest of fruits of *L. cymosa* strongly reflect their home range size and group size. *S. nigricollis,* with home ranges of 40-50 ha, visited the plots more frequently than *S. sciureus,* ranging through a twenty fold bigger area (of up to 1000 ha). Traveling through the study plots, the small family groups of *S. nigricollis* (up to 9 individuals) visited and exploited only a small number of trees per day and consumed not more than 25 fruits per tree. As can be seen in Figures 8 a) and b), fruit removal by *S. nigricollis* did not markedly influence the standing crop of ripe fruits in the plots. Groups of *S. sciureus*, which consist of 20-50 individuals, exploited more trees when crossing a study plot and were able to harvest a large amount of the ripe fruits of *L. cymosa*, especially when such a group met a large patch of *L. cymosa*-trees. For example, two visits of *S. sciureus* in plot **HL** during a count interval of 6 days were sufficient to remove 50% of the standing crop of ripe fruits of *L. cymosa* in this plot.

The time pattern of fruit removal of each of the two monkey species can also be related to their different home range size and traveling habits. Fruit removal by *S. sciureus* was very pronounced at the times of highest standing crop. Such harvesting peaks seem to result from groups of the squirrel monkeys traveling “at the right time” (= high standing crop) “on the right line” (= taking a route on which they pass by a high number of *L. cymosa*-trees). Low fruit consumption despite of high fruit offer coincided with longer periods of absence of *S. sciureus* from the plot, like in the interval before the peak in **HL** and the two intervals after the peak in **P**. Fruit removal by the almost resident *S. nigricollis* was more distributed over the whole fruiting season, and their harvesting activity showed an overall upward tendency from the beginning towards the end of the fruiting season.

Other mechanisms than range and group size might also play a role in determining the time pattern of exploitation of the fruit resource offered by *L. cymosa*. In 1999, when the monitoring of fruiting covered a longer period than in 2000, and when fruit ripening spread over a longer period than in 2000, I observed a striking rise of fruit consumption by *S. sciureus* and *S. nigricollis* in March. The monkeys did not show interest in harvesting fruits of *L. cymosa* before, although 50% of the total number of ripe fruits in the respective season had already been produced by the trees up to that date. This kind of non-linear fruit consumption pattern, restricted to times of high standing crops, might result from staggered fruiting phenology of several important food trees used by the two monkey species, including *L. cymosa*. Staggered fruiting phenologies can result from inter-specific competition of plant species that share the same frugivore species (or species assemblage), like it seems to be the case in trees of the genus *Miconia* in Panama. These trees produce moderate numbers of fruits and are mainly consumed by locally resident manakins (birds), so inter-specific competition for frugivores is high. Fourteen *Miconia* species of this genus show clearly segregated fruiting phenologies (Poulin et al. 1999). I did not study the fruiting phenologies of other species than *L. cymosa* in detail, so I lack the information of how exactly fruiting of *L. cymosa* fits into the fruiting of other food species of *S. sciureus* and *S. nigricollis*. However, there is no indication of a “shortage” in other fruit supply that would make *S. sciureus* and *S. nigricollis* shift abruptly to *L. cymosa*. Fruiting of *L. cymosa* occurs during the main fruiting period of the forest in Cuyabeno (Figure 9). I found another 8 species of trees which also belong to the diet of *S. nigricollis* and *S. sciureus*, and fruit at the same time like *L.* cymosa (Appendix B).

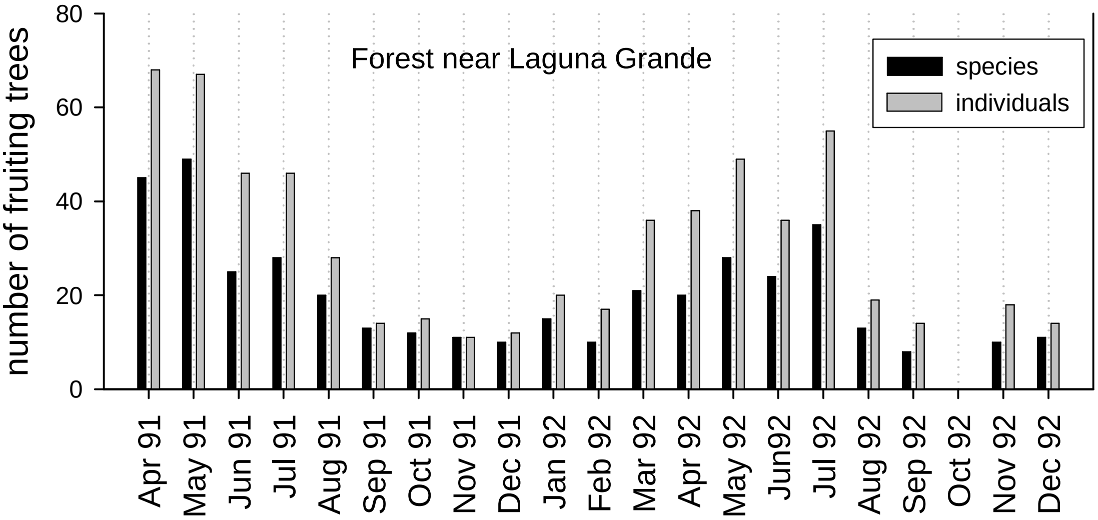

Figure 9: Fruiting phenology of the forest in the study area (bar chart from de Vries et al. (1993) based on a 1800 m-transect close to my study sites).

The disperser system of *L. cymosa*

L. cymosa trees in Cuyabeno seem to depend for dispersal of their seeds on a few individuals of a small number of frugivorous species. The only reliable disperser that could be identified so far in this study is *Saguinus nigricollis*. This species depends to a large extent on fruit diet (Ulloa 1988; Emmons 1990; de la Torre 1991; Garber 1993; Peres 1993; de la Torre et al. 1995; Lima et al. 2003). Thus, the criteria of a “specialist dispersal system” (Howe 1993) apply to *L. cymosa*, for both the plant side and the frugivore. This even holds true if one assumes that bats were part of *L. cymosa*’s disperser assemblage.

S. nigricollis is obviously an important disperser for *L. cymosa*. How important is *L. cymosa* for *S. nigricollis*, on the other hand? Are there indications for tamarins feeding preferentially on *L. cymosa*? A variety of field observations support this idea. In Peru, fruits of the genus *L. cymosa* ranked as no. 12 in terms of harvesting frequency of 73 fruit species consumed by *Saguinus fuscicollis* (Knogge 1999). In Brazil *S. fuscicollis* showed preference for *Leonia* spp. too, visiting trees of this species ten times more frequently than expected based on its abundance (Peres 1993). *Leonia glycicarpa*, having bigger but otherwise similar fruits to *L. cymosa*, is mentioned by Terborgh (1983) as a fruit often taken by *Saguinus*. Tamarins also seem to eat other large-seeded fruits. The size distribution of seeds from fruits consumed by *S. fuscicollis* was shown to peak at a seed size of 16-18 mm (see figure 7, from Knogge 1999). Because it is a close relative and similar in size, there is reason to assume that *S. nigricollis* shows similar feeding habits. The seeds of *L. cymosa*, having a mean size of 13 mm would fit very well into this distribution. It has been hypothesized by Garber (1997) that tamarins might indeed need to ingest large seeds for mechanically dislodging and expelling spiny-headed worms from their intestine (tamarins are infested with worms by feeding on Orthopterans). A preference for large-seeded fruits would make *Saguinus* a more reliable disperser, and might provide a basis for a co-evolution with fruit or plant traits. Yet, tamarins might not prefer large-seeded fruits but simply feed on the fruits available. In the mid storey of a Venezuelan rain forest, for example, Schaefer (2002) found almost exclusively large fruits, whereas small fruits were restricted to the ground and canopy level. If seed size is positively correlated with fruit size (Niklas 1994), feeding on large-seeded fruits might simply reflect the availability of fruits at the foraging height of *Saguinus*. Whether availability or preference, it seems clear that (1) the tamarin diet contains largely of large-seeded plant species, (2) fruits of *L. cymosa* are very attractive to tamarins, and (3) tamarins give reliable dispersal service to *L. cymosa*. To conclude, there seems to exist a close interaction between *S. nigricollis* and *L. cymosa*.

The feeding activity of squirrel monkeys, which remove large quantities of fruits without dispersing seeds, may have an impact on the fruit ripening regime of *L. cymosa*. Extended ripening seasons in trees with small to middle sizes of fruit crop and a small assemblage of reliable dispersers have been pointed out as strategies to avoid saturation of dispersers (Howe et al. 1977, for bird-dispersed trees). The mammal-dispersed *L. cymosa* shows exactly such a ripening regime (see chapter 3.1). However, its slow way of fruit ripening over a prolonged period of time, as opposed to synchronous ripening, might also be interpreted as a strategy to avoid “loosing” too many fruits in just one visit by squirrel monkeys. This strategy might improve chances to provide as many fruits as possible to reliable dispersers, limiting the loss to fruit “thieves”.

References

de la Torre, S. (1991) Area de vida, comportamiento reproductivo y habitat de *Saguinus nigricollis graellsi* (Primates: Callitrichidae) en la Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 162

de la Torre, S., F. Campos and T. de Vries (1995). Home range and birth seasonality of *Saguinus nigricollis graellsi* in Ecuadorian Amazonia. American Journal of Primatology 37: 39-56.

de Vries, T., F. Campos, S. de la Torre, E. Asanza, A. C. Sosa and F. Rodriguez (1993). Investigación y conservación en la Reserva de Producción Faunistica Cuyabeno. La investigación para la conservación de la diversidad bilógica en el Ecuador. Memorias del simposio llevados cabo del 10 al 12 de junio de 1992, Quito, Ecosciencia.

Ebigbo, N. M. (2004). The role of flying foxes as seed dispersers. On the vegetation dynamics in a West African forest-savanna mosaic in Côte d'Ivoire. Fakultät für Naturwissenschaften. Ulm, Universität Ulm: 140.

Emmons, L. H. (1990). Netropical Rainforest Mammals: A Field Guide. Chicago and London, The University of Chicago Press.

Feldmann, M. (2000). Samenökologie von Parkia im Amazonas-Regenwald. Samenausbreitung durch Krallenaffen (Callitrichidae), sekundäre Ausbreitung von Samen und Samenprädation. Institut für Zoologie und Anthropologie. Göttingen, Georg-August-Universität: 105.

Forget, P. M., T. Milleron and F. Feer (1998). Patterns in post-dispersal seed removal by neotropical rodents and seed fate in relation to seed size. Dynamics of tropical Communities. The 37th symposium of the British Ecological Society Cambridge University. D. M. Newbery, H. H. T. Prins and N. D. Brown, Blackwell Science: 25-49.

Garber, P. A. (1993). Feeding ecology and behavior of the genus Saguinus. Marmosets and Tamarins. Systematics, Behavior, and Ecology. A. B. Rylands. New York, Oxford University Press: 273-295.

Garber, P. A. and U. Kitron (1997). Seed swallowing in tamarins: evidence of a cuarative function or enhanced foraging efficiency? International Journal of Primatology 18: 523-538.

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.

Hammond, D. S. (1995). Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexixo. Journal of Tropical Ecology 11: 295-313.

Hovestadt, T. (1997). Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des Comoé Nationalparks, Elfenbeinküste.1. Aufl. Berlin, Wissenschaft und Technik Verlag.

Howe, H. F. (1986). Seed dispersal by fruit-eating birds and mammals. Seed dispersal. D. R. Murray, Academic Press, Australia: 123-189.

Howe, H. F. (1993). Specialized and generalized dispersal systems: where does 'the paradigm' stand? Vegetatio 107/108: 3-13.

Howe, H. F. and G. F. Estabrook (1977). On intraspecific competition for avian dispersers in tropical trees. American Naturalist 111: 817-832.

Howe, H. F. and J. Smallwood (1982). Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13: 201-228.

Izawa, K. (1978). A field study on the ecology and behavior of the Black-mantle tamarin (Saguinus nigricollis). Primates 19: 241-274.

Kalko, E. K. V. and M. A. Condon (1998). Echolocation, olfaction and fruit display: how bats find fruit of flagellichorous cucurbits. Functional Ecology 12: 364-372.

Kalko, E. K. V., E. A. Herre and C. O. Handley (1996). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. Journal of Biogeography 23: 565-576.

Kinzey, W. G. (1997). New world primates: ecology, evolution, and behavior. New York, de Gruyter.

Knogge, C. (1999). Tier-Pflanze-Interaktion im Amazonas-Regenwald: Samenausbreitung durch die sympatrischen Tamarinarten Saguinus mystax und Saguinus fuscicollis (Callitrichidae, Primates). Münster, Schüling Verlag.

Korine, C., E. K. V. Kalko and E. A. Herre (2000). Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. Oecologia 123: 560-568.

Lima, E.-M. and S.-F. Ferrari (2003). Diet of a free-ranging group of squirrel monkeys (Saimiri sciureus) in eastern Brazilian Amazonia. Folia Primatologica 74: 150-158.

McKey, D. (1975). The ecology of coevolved seed dispersal systems. Coevolution of animals and plants. L. E. Gilbert and P. H. Raven. Austin, Texas, University of Texas Press: 159-191.

Müllner, A. and A. Pfrommer (2001). Regenwaldtourismus und sein Einfluss auf ausgewählte Wildtierarten am Río Cuyabeno. Roßdorf, TZ-Verlagsgesellschaft mbH.

Niklas, K. J. (1994). Plant Allometry. Chicago, University of Chicago Press.

Peres, C. A. (1993). Diet and feeding ecology of saddle-back (Saguinus fuscicollis) and moustached (S. mystax) tamarins in an Amazonian terra firme forest. J. Zool., Lond. 230: 567-592.

Peres, C. A. (1993). Structure and spatial organization of an Amazonian terra firme forest primate community. Journal of Tropical Ecology 9: 259-276.

Poulin, B., S. J. Wright, G. Lefebvre and O. Calderón (1999). Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. Journal of Tropical Ecology 15: 213-227.

Schaefer, H. M. and V. Schmidt (2002). Vertical stratification and caloric content of the standing fruit crop in a tropical lowland forest. Biotropica 34: 244-253.

Snow, D. W. (1971). Evolutionary aspects of fruit-eating birds. Ibis 113: 194-202.

Terborgh, J. (1983). The use of plant resources (chapter 5), Foraging for prey (chapter 6). Five new world primates: a study in comparative ecology. J. Terborgh. Princeton, N.J., Princeton Univ. Pr.

Thies, W., E. K. V. Kalko and H. U. Schnitzler (1998). The roles of echolocation and olfaction in two Neotropical fruit-eating bats, Carollia perspicillata and C-castanea, feeding on Piper. Behavioral Ecology and Sociobiology 42: 397-409.

Ulloa, R. (1988) Estudio sinecologico de primates en la Reserva de Producción Faunistica Cuyabeno, Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 179

van der Pijl, L. (1969). Principles of dispersal in higher plants. Berlin, Springer.

Walther, B. A. (2002). Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. Journal für Ornithologie 143: 64-81.

Wheelwright, N. and G. Orians (1982). Seed dispersal by animals - contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist 119: 402-413.

4 Interaction of plant and monkeys

4.1 Does the quality of fruits of *Leonia cymosa* (Violaceae) influence fruit choice by its free ranging reliable seed disperser *Saguinus nigricollis* (Callitrichidae)?

Abstract

The nutritional contents of the fruit pulp might be an important factor influencing monkeys' fruit choice and thus be a key factor determining the fruits removed from individual trees by reliable seed dispersers. In *Leonia cymosa*, *Saguinus nigricollis* was identified as feeding on the fruits and being a reliable seed disperser. I investigated whether fruit removal correlated with content of fructose, glucose, sucrose, total protein (pulp does not contain lipids) or total metabolisable energy, seed to pulp ratio, or water content. No significant correlations were found after correction for multiple tests. However, the single test showed a positive influence of pulp to seed ratio on fruit removal by *S. nigricollis*. Feeding preferences for single sugars determined by other laboratory studies were not confirmed by this field study. It might be possible that other compounds in the fruit pulp not measured or other tree traits or neighborhood conditions overlay the effect of nutrients on fruit removal. The reliable seed disperser *S. nigricollis* does not seem to exert selective pressure on nutrient content of the fruits of *L. cymosa*.

4.1.1 Introduction

Animals should try to optimize food intake by selection of food items that yield most energy and/or essential nutrients per unit handling time. This fundamental prediction of the optimal diet theory (ODT, Stephens et al. 1986) applies especially to foragers of non mobile prey (Sih et al. 2001). Among non mobile prey items, fruits have rarely been at the focus of field studies deduced from ODT, which is surprising because fruits are a "non-cryptic prey item that is meant to be eaten" (Schaefer 2002, synopsis). Nevertheless, there is evidence from a broad range of taxa that frugivores behave in accordance with ODT: fruits eaten by spider monkeys (*Ateles geoffroyi*) had higher sugar contents than fruits available at the same time, but not eaten (Riba-Hernandez et al. 2003), intake of lipids from fruits and leaves was exceptionally high in white-faced sakis (*Pithecia pithecia*)

(Norconk et al. 2004), baboons (*Papio anubis*) preferred fruits high in protein content and low in fiber and phenolics (Barton et al. 1994), ground storey frugivorous bats selected fruits high in nutrient content (Bonaccorso et al. 1987), and fat-tailed dwarf lemurs (*Cheirogaleus medius*) selectively fed on sugar rich fruits during fat storing period before hibernation (Fietz et al. 1999). Fruit removal by birds in a community of fruiting trees in the rainforest of Venezuela was explained by macro-nutritional contents (sugar, lipid, protein), while phenols and water deterred removal (Schaefer et al. 2003). This implies that feeding preferences of dispersers should finally lead to differential recruitment of different plant species as well as of different individual plants within a species according to their fruit quality. In all examples cited above from the literature, choices between different fruit species were the study focus. To my knowledge, studies on fruit selection within a plant species are almost lacking, although they could give further insights into the question how frugivores exert selective pressure on fruit traits.

Within a fruiting plant species, selection of profitable fruits by dispersers would have implications for individual fitness. Individuals providing fruits with more nutrients – especially those matching preferences of reliable dispersers – should gain a higher dispersal success than those with less nutritional content because dispersers should harvest larger amounts of the more profitable fruits. Only Foster (1990) and Schaefer (2002, chapter 5) related within-species variation of fruit quality with fruit removal. While Foster did not find correlations of nutritional content of fruits with feeding rates of birds in a subtropical tree, Schaefer (2002, chapter 5) could show that birds feeding on *Goupia glabra* (Celastraceae) in a Venezuelan tropical forest maximized their instantaneous rate of energy gain and avoided unripe fruits. However, this study focused on the bird's perspective and did not address consequences for seed dispersal from the perspective of the individual plant. Here, I link an analysis of macronutrients in the fruit pulp with individual dispersal success, defined as fruits removed by the reliable seed disperser from an individual tree during an entire fruiting season.

My study object was the tree *Leonia cymosa* (Violaceae) from the under storey of the east Ecuadorian rain forest. Individual trees showed clearly distinguishable compositions of the readily assimilable sugars fructose, glucose and sucrose in the fruit pulp, as well as individual protein contents (see Chapter 3.1; fruit pulp does not contain lipids). In my study area, fruits of *L. cymosa* were mainly removed by Squirrel monkeys (*Saimiri sciureus*) and by black mantle tamarins (*Saguinus nigricollis*). Among these only *S. nigricollis* dispersed the seeds by swallowing seeds together with fruit pulp (see Chapter

3.2). I therefore focus here on *S. nigricollis* because I expected feeding preferences of this reliable disperser to have a stronger selective effect on the nutritional content of fruit of *L. cymosa* than a non-disperser. Fruit choice based on nutritional profitability of fruits should be possible in *S. nigricollis*, because it is very likely that it has a highly sensitive sense of taste for the sugars present in *L. cymosa*-fruits, and might be especially stimulated by fructose and sucrose, like several other species of the genus *Saguinus* (Glaser 1986; Simmen 1992; Simmen et al. 1998).

Considering nutrient discrimination capacities and goal-oriented foraging in *Saguinus* (Garber 1988; Garber 1993) I hypothesized that fruit selection based on profitability criteria would lead to differential fruit removal by *S. nigricollis* in *L. cymosa*-trees of comparable fruit crop size. I observed fruit removal by *S. nigricollis* during an entire fruiting season in six trees with large seasonal fruit crop sizes that were located in one study plot and visited by only one group of *S. nigricollis*. This made it possible that tamarins revisited a single tree several times after finding out about its nutritional offer at the first feeding visit. I tested if seasonal fruit removal correlated with the content of either single nutritional components, or total energy content, or water content, or the ratio of pulp to seed mass. I expected fructose and sucrose to influence fruit removal by *S. nigricollis*. As the tamarins swallow seeds together with fruit pulp, I expected that they prefer fruits with a large pulp to seed mass ratio.

4.1.2 Methods

Study site

L. cymosa-trees were studied in plot **P** in terra firme forest in the vicinity of the Laguna Grande de Cuyabeno (0°2'N 76°15'W, elevation 250 m), located within the Cuyabeno Faunistic Reserve in north-eastern Ecuador (for detailed a description of the study area see chapter 2).

Fruit production and harvest

Fruit production and fruit harvest by monkeys were monitored during 6 weeks from April to May 2000 by weekly fruit counts and daily revisions of trees for peels remaining under the trees after feeding visits (for details of counting techniques and accounting methods see chapter 3.1.5 and 3.2.3). The complete fruiting tree population of study plot **P** was included into the counts. Censuses of monkey density revealed that each study plot formed part of the home range of one group of *S. nigricollis* (see chapter 3.2.2). I determined fruit consumption by *S. nigricollis* by combining characteristics of peel fragments and the state of seeds found below trees with the daily spatial pattern of feeding events and the amount of fruits removed per tree or patch (as described in detail in 3.2.3). The seasonal fruit crop size of an individual tree is the sum of all ripe fruits produced by this tree during the fruiting season. Likewise, the total number of fruits removed from each tree during the fruiting season was determined by summing up all fruits consumed in all single feeding events.

Fruit sampling

I sampled fruits once per tree in early May (i.e. towards the end of the fruiting period). I picked 10 fruits per tree from different branches distributed all over the tree crown in order to take into account the within tree variation of fruit quality. Fruits grow on younger twigs in the outer tree crown layer. All fruits picked were ripe (= in the yellow colour state), of medium size (approx. 2 cm in diameter) and of most similar condition (e.g. softness). Fruits were taken to the field lab within 1- 2 hours, where pulp samples were prepared immediately.

It is known from intensive research in horticulture and agriculture that most fruit characteristics and the process of fruit ripening itself are quantitatively inherited (Grandillo et al. 1999; Giovannoni 2001; Li et al. 2005). Therefore the ripe fruits of an individual of *L. cymosa* should constantly have a tree-specific quality. It is possible that climatic variation in the course of the fruiting season caused a variation in fruit quality, additional to the genetically determined fruit quality. However, climatic conditions were the same for all trees observed and any climatic effect on fruit ripening should be largely the same in all trees observed. Thus, the fruit quality of a tree determined at the moment of fruit sampling is very likely representative for its fruit quality throughout the whole fruiting season relative to other tree individuals.

Nutritional analysis of fruits

I measured the diameter of the fruits, separated the pericarp from the fruit pulp and seeds and weighed the fruit pulp-seed-compound with a Mettler PJ 300 balance (accuracy: 0.001 g). I separated fruit pulp from seeds and measured its fresh weight. Total seed mass (fresh weight) per fruit was calculated by subtracting fruit pulp weight from the weight of the pulp-seed compound. Fruit pulp was conserved in the field in approx. 5-7 ml ethanol (98%) in 10 ml-scintillation bottles of known weight. In the laboratory the ethanol was volatilized. Samples were then further dried inside a drying closet at 35-40°C until weight stayed constant. Dry weight of the fruit pulp samples was eventually determined by subtracting the weight of the bottles. Subsequently, I added a defined volume of double-distilled water (between 5 and 15 ml, according to pulp weight) to the dry fruit pulp and ethanol extract still in the scintillation bottles. Dry ethanol extract was completely soluble in water, thus indicating the absence of lipids in the fruit pulp. The pulp was homogenized in this water using an ULTRA-TURRAX®. The homogenate was then used for further analysis. Content of fructose, glucose and sucrose were analyzed by HPLC, and protein content by a photometric BCA protein assay (for details see chapter 3.1.4.1). I calculated total energy content of the fruit pulp (kJ / g dry weight) using the following conversion factors: 17 kJ/g for carbohydrates and 17 kJ/g for proteins (Karlson 1984).

Data analysis

I define dispersal success as the total of fruits removed by the reliable seed disperser *Saguinus nigricollis* (Callitrichidae) from the total seasonal production of ripe fruits of a tree. I think that this integration of fruit harvest is a good estimate of tree preference because it includes a potential learning of profitable food sources. The absolute amount of fruits removed by *S. nigricollis* is a better estimate of a tree's success of dispersal by *Saguinus* than the proportion of the total seasonal fruit crop removed because I attempted to control for fruit crop size by observing only trees with exceptionally large fruit crop sizes (see figure 18, chapter 3.1). *S. nigricollis* remove only small numbers of fruits per visit. Thus tamarins find ripe fruits "ad libitum" in trees considered here, which had maximum weekly standing crops of 65 to 226 ripe fruits. It is therefore more reasonable to look at the number of fruits consumed than to relate fruit consumption with production by forming proportions.

From the ten fruits sampled per tree, I calculated median values of content of the respective nutritional components, of total energy content, of water content, and of the ratio of pulp to seed mass. To test for correlations between these median values and the total number of fruits removed in a tree I used Spearman's rank correlations calculated in Statistica 5.5 (StatSoft, Inc. 2000). Spearman's rank correlations were also used to detect co-variation of single nutrient components and fruit characters. I corrected for multiple testing using the Dunn-Šidák method (Sokal 1995) to adjust α -values. *S. nigricollis* did not remove fruits from one of the six trees at all (tree no. p06). I excluded this tree from the analysis because it did not meet the condition that tamarins should have consumed fruits at least once during my study to be able later to make a choice based on taste and profitability of the fruits. None the less, I listed the nutrient content values of this tree together with the other trees in the appendix C. It is still possible that not consuming fruits of this tree reflected a choice based on previous experience of the monkeys.

4.1.3 Results

Fruit removal by *S. nigricollis* was neither correlated with the content of single sugars, nor with the total of soluble sugar (see Table1 for test results). Fruit removal did also not correlate with total energy content of the fruits, because the total energy content of the fruits mainly resulted from sugar. Fruit removal was not correlated with water content, either. Applying the conservative method of correcting for multiple testing, fruit removal by *S. nigricollis* did not show a correlation with protein content of the fruit pulp, nor with the ratio of pulp mass to seed mass.

Table 1: Summary of Spearman's rank correlation tests for correlations of fruit consumption by *Saguinus nigricollis* with median nutrient contents and medians of other profitability parameter of fruits of five trees of *Leonia cymosa*.

		n	R	t(n-2)	p-level	adjusted p-level*
Number of fruits consumed by *Saguinus nigricollis* vs.						
	Fructose	5	-0.3	-0.545	0.6	n.s.
	Glucose	5	-0.3	-0.545	0.6	n.s.
	Sucrose	5	0.7	1.698	0.2	n.s.
	Total soluble sugar	5	0.0	0.0	1.0	n.s.
	Protein	5	-0.9	-3.576	0.04	n.s
	Energy	5	-0.1	-0.174	0.9	n.s.
	Water	5	0.7	1.698	0.2	n.s.
	Pulp mass / seed mass	5	0.9	3.576	0.04	n.s.

***** Dunn-Šidák method (Sokal 1995)

4.1.4 Discussion

In a set of trees of *Leonia cymosa* with distinct, individual fruit quality, fruit removal by the free ranging reliable seed disperser *Saguinus nigricollis* was not attributable to contents of single nutrients or energy content of their fruits. Against my prediction, neither fructose nor sucrose seemed to influence fruit choice of tamarins and thus their preference for individual trees of *Leonia*. This is surprising, because in laboratory experiments with other species of the genus *Saguinus* both sugars were very effective feeding stimulants (Glaser 1986; Simmen 1992). Taste thresholds of these *Saguinus*-species determined by two solution choice tests against sugar-free water ranged from 0.18% to 1.2% solution (weight/volume) fructose and from 0.55% to 4.3% sucrose (Glaser 1986, determined by a two solution choice test against sugar free water; Simmen 1992; Simmen et al. 1998). The median fructose concentrations in fruits of all trees sampled (see Appendix C) were way over these taste threshold concentrations. Only in one tree the median sucrose concentrations of its fruits was below the upper taste threshold concentration of sucrose known from the laboratory (with 3.7% sucrose solution in fruits vs. 4.3% taste threshold sucrose solution in laboratory tests). Thus, if the taste thresholds of *S. nigricollis* fall into the actually known range of its genus, *S. nigricollis* should be capable of tasting both sugars in the fruits of *L. cymosa*.

It seems that despite of sufficiently high sugar concentrations in the fruits of *L. cymosa* tamarins did not strongly diffentiate between trees of different fruit quality. *S. nigricollis* might either have preferences for different sugars than other species of the genus, or free ranging tamarins react differently on sugars than caged tamarins. Such a discrepancy between laboratory and field results has been noted in spider monkeys (*Ateles geoffroyi*). This species showed preference for sucrose rich diet in feeding experiments (Laska et al. 1996; Laska et al. 1998). However, free ranging spider monkeys consumed fruit species with significantly higher concentrations of glucose and fructose than sucrose, and at the intra-specific level, food-fruits had significantly more fructose and glucose than non-food fruits, but no difference was found for sucrose (Riba-Hernandez et al. 2003). Thus *Ateles* optimized sugar intake, but not of the sugar preferred in feeding trials. *S. nigricollis* on the other hand did not seem to optimize nutrient intake while feeding on *L. cymosa*. Yet, it cannot be ignored that the data show some correlation of fruit removal with pulp to seed ratio (p=0.04 if not corrected for multiple tests), and of protein, which covaries negatively with the pulp to seed ratio (see Appendix D). Such a correlation might possibly be confirmed with a greater sample size. Possibly, *S. nigricollis* might try to get as much pulp as possible per unit food, without so much caring for the differences in content of the main nutrient components of the fruits. It is possible that nutrients not measured, like for example minerals play a role in feeding decisions of *S. nigricollis* on *L. cymosa*. However, in this case tamarins would have to be able to taste minerals and to distinguish mineral contents at low concentrations. To date, the sense of taste of tamarins concerning minerals is not yet investigated.

Field studies on primate feeding strategies with special respect to nutrient intake are rare (e.g. Fietz et al. 1999; Riba-Hernandez et al. 2003). Studies of free ranging tamarins from the genus *S. nigricollis* at least show that the diet of free ranging primates of tropical rain forests is very diverse (Terborgh 1983; de la Torre 1991; Peres 1993; Knogge 1999; Lima et al. 2003). Consuming the fruits of *L. cymosa*, regardless of variation of individual trees, could still reflect fruit choice in accordance with ODT because *Leonia* might be rich in sugar and protein relative to other fruit resources available at the same time. It is non the less puzzling that *S. nigricollis* seemed not to forage according ODT as far the single food species *L. cymosa* was concerned, because they did not preferentially feed on those *L. cymosa*-trees with high nutrient contents in their fruits. It is possible that the within tree variation in fruit quality might have hindered clear-cut discrimination of trees, or other chemical components like fruit acids, might conceal sugar taste. However, for humans the fruit pulp of *L. cymosa* does not have a sour taste.

In the diet of *S. nigricollis, L. cymosa* might also form a component that does not support the energy budget but serves other purposes unknown to me. Also, other factors than nutritional quality of the fruits might influence the tamarin’s choice of tree individuals. For example, predation risk in a tree, spatial position and accessibility of a tree as well as growth traits might override the influence of nutrients on fruit removal. Trade-offs between nutrient gain and effort to access fruits have so far been demonstrated experimentally in captive Neotropical tanagers (Moermond et al. 1983). Also, neighborhood conditions influenced fruit removal by birds (Sargent 1990). My intent to reduce variation introduced by such factors by choosing trees of comparable fruit crop size and growth might have failed. I studied the effect of tree traits and neighborhood conditions on fruit harvest in a separate approach using a larger tree sample size. The results are presented in the following chapter 4.2.

In the interaction of zoochorous plants and frugivores, one would expect mainly the reliable disperser to exert selective pressure on nutritional content of the fruits, because their food choice has direct consequences for the recruitment of the plants. Tamarins, the reliable dispersers with high affinity towards *L. cymosa*, were found to be less choosy than expected. The data from a limited number of *L. cymosa* trees studied here do not support my hypothesis of a differential dispersal success of individual trees mediated through fruit nutrient content. Energy content and /or other potential contents of *Leonia* fruits are obviously sufficient to make them attractive to tamarins. The nutritional profile of the fruits of *Leonia* might be shaped rather by the whole assemblage of fruit users than by a single disperser species. My study also underlines the importance of field studies to separate between sensorial abilities of fruit users and the realized behavior in the wild.

References

Barton, R. A. and A. Whiten (1994). Reducing complex diets to simple rules - food selection by olive baboons. Behavioral Ecology and Sociobiology 35: 283-293.

Bonaccorso, F. J. and T. J. Gush (1987). Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: an experimental study. Journal of Animal Ecology 56: 907-920.

de la Torre, S. (1991) Area de vida, comportamiento reproductivo y habitat de *Saguinus nigricollis graellsi* (Primates: Callitrichidae) en la Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 162

Fietz, J. and J. U. Ganzhorn (1999). Feeding ecology of the hibernating primate Cheirogaleus medius : how does it get so fat? Oecologia 121: 157-164.

Foster, M. S. (1990). Factors influencing bird foraging preferences among conspecific fruit-trees. Condor 92: 844-854.

Garber, P. A. (1988). Foraging decisions during nectar feeding by tamarin monkeys (Saguinus mystax and Saguinus fuscicollis, Callitrichidae, Primates) in Amazonian Peru. Biotropica 20: 100-106.

Garber, P. A. (1993). Feeding ecology and behavior of the genus Saguinus. Marmosets and Tamarins. Systematics, Behavior, and Ecology. A. B. Rylands. New York, Oxford University Press: 273-295.

Giovannoni, J. (2001). Molecular biology of fruit maturation and ripening. Annual Review of Plant Physiology and Plant Molecular Biology 52: 725-749.

Glaser, D. (1986). Geschmacksforschung bei Primaten. Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 131: 92-110.

Grandillo, S., H. M. Ku and S. D. Tanksley (1999). Identifying the loci responsible for natural variation in fruit size and shape in tomato. Theoretical and Applied Genetics 99: 978-987.

Knogge, C. (1999). Tier-Pflanze-Interaktion im Amazonas-Regenwald: Samenausbreitung durch die sympatrischen Tamarinarten Saguinus mystax und Saguinus fuscicollis (Callitrichidae, Primates). Münster, Schüling Verlag.

Laska, M., E. C. Sanchez and E. R. Luna (1998). Relative taste preferences for food-associated sugars in the spider monkey (Ateles geoffroyi). Primates 39: 91-96.

Laska, M., E. C. Sanchez, J. A. R. Rivera and E. R. Luna (1996). Gustatory thresholds for food-associated sugars in the spider monkey (Ateles geoffroyi). American Journal of Primatology 39: 189-193.

Li, L., J. Strahwald, H. R. Hofferbert, J. Lubeck, E. Tacke, H. Junghans, J. Wunder and C. Gebhardt (2005). DNA variation at the invertase locus invGE/GF is associated with tuber quality traits in populations of potato breeding clones. Genetics 170: 813-821.

Lima, E.-M. and S.-F. Ferrari (2003). Diet of a free-ranging group of squirrel monkeys (Saimiri sciureus) in eastern Brazilian Amazonia. Folia Primatologica 74: 150-158.

Moermond, T. C. and J. C. Denslow (1983). Fruit choice in Neotropical birds: effects of fruit type and accessibility on selectivity. Journal of Animal Ecology 52: 407-420.

Norconk, M. A. and N. L. Conklin-Brittain (2004). Variation on frugivory: The diet of Venezuelan white-faced sakis. International Journal of Primatology 25: 1-26.

Peres, C. A. (1993). Diet and feeding ecology of saddle-back (Saguinus fuscicollis) and moustached (S. mystax) tamarins in an Amazonian terra firme forest. J. Zool., Lond. 230: 567-592.

Riba-Hernandez, P., K. E. Stoner and P. W. Lucas (2003). The sugar composition of fruits in the diet of spider monkeys (Ateles geoffroyi) in tropical humid forest in Costa Rica. Journal of Tropical Ecology 19: 709-716.

Sargent, S. (1990). Neighborhood effects on fruit removal by birds: a field experiment with Viburnum dentatum (Caprifoliaceae). Ecology 71: 1289-1298.

Schaefer, H.M. (2002) The influence of fruit pulp chemistry on avian fruit choice. Dissertation, Fachbereich Biologie, Geo- und Umweltwissenschaften, Universität Oldenburg, Oldenburg, pp 114

Schaefer, H. M., V. Schmidt and H. Winkler (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. Oikos 102: 318-328.

Sih, A. and B. Christensen (2001). Optimal diet theory: when does it work, and when and why does it fail? Animal Behavior 61: 379-390.

Simmen, B. (1992). Taste thresholds and above-threshold responses to fructose in callitrichid primates with reference to diet. Comptes Rendus de l'Academie de Sciences Série III Sciences de la Vie 315: 151-57.

Simmen, B. and C. M. Hladik (1998). Sweet and bitter taste discrimination in primates: scaling effects across species. Folia Primatologica 69: 129-138.

Stephens, D. W. and J. R. Krebs (1986). Foraging Theory. Princeton, New Jersey, Princeton University Press.

Terborgh, J. (1983). Five new world primates: a study in comparative ecology. Princeton, Princeton University Press.

4.2 Fruit removal by monkeys from a Neotropical tree: a test of the fruit crop size hypothesis

Albrecht Pfrommer and K. Eduard Linsenmair

Abstract

The fruit crop size hypothesis (FCSH) predicts that seed-dispersing frugivores exert selective pressure on the fruit crop size of fleshy-fruited plants. It has been developed mainly with reference to bird-dispersed plants. We evaluated the FCSH for the monkey-dispersed tree *Leonia cymosa* (Violaceae) in the rain forest of Amazonian Ecuador. Tamarins, *Saguinus nigricollis*, and squirrel monkeys, *Saimiri sciureus*, consumed fruits of this tree, with only the former dispersing the seeds. The probability of visits by tamarins, and the number of fruits they removed throughout the fruiting season increased with growing seasonal fruit crop size, while the proportion of fruits they removed decreased. Tamarins less likely harvested trees the more open these stood in the under storey, probably to avoid predation by forest raptors. High conspecific fruit offer in the neighborhood of a tree reduced the proportion of fruits removed from it by tamarins, indicating competition for seed dispersers. Our results suggest selection of the disperser on fruit crop size of *L. cymosa*, yet predation risk at a particular site, and fruit offer in the neighborhood may constrain selective pressures. Fruit removal by tamarins followed the FCSH. However, the mechanism favoring large fruit crop sizes was different to that assumed by the FCSH. Large fruit crops do not represent more profitable fruit resources, because of the tamarins' very limited food uptake capacity per visit. Therefore, rather an enhanced visual appearance and the possibility of being repeatedly harvested favor large fruit crop sizes. All aspects of fruit removal by squirrel monkeys were positively linked to growing seasonal fruit crop size. This renders it possible that the non-disperser as well exerts selection pressure on fruit crop sizes of this tree. Opposed to the view that contrasting responses of frugivores to fruit and fruit display traits lead to inconsistent selection, this study shows that in the same plant seed dispersers and other frugivores not dispersing seeds may exert concordant selection pressures.

4.2.1 Introduction

Seed dispersal is crucial for plant fitness (Wang and Smith 2002). Dispersal success is often directly linked to plant reproductive success due to the prevalent density dependent mortality of seeds and seedlings (Janzen 1970; Connell 1971; Harms et al. 2000). A large proportion of trees in tropical rain forests are fleshy fruited, and depend on fruit removal by frugivorous animals and their reliably dispersing seeds away from the mother plant (Howe and Smallwood 1982; Jordano 2000). Fruit removal by animals consists of two steps: detection of a fruit resource and harvesting it (Murray 1987). Both steps (and subsequent seed dispersal) can only function properly if fruit and plant traits correspond to the sensory and morphological capacities of the frugivores. Contrasting fruit colors, for example, make fruits detectable for birds but not for nocturnal bats. In contrast, bats often use smell for far-range detection of fruiting trees (Korine et al. 2000).

Despite the known mutual interdependence of plants and frugivores, it is still controversial if plant fruiting traits evolve under the selective influence of dispersers. The assemblage of fruit users often includes many species with varying specialization on frugivory and different, sometimes contrasting feeding preferences. It has been proposed that the diversity of frugivore preferences leads to an inconsistent overall selective influence of frugivores on the expression of fruit traits (Wheelwright and Orians 1982 ; Herrera 1985, both reviewing criticism on species-to-species interaction of plants and frugivores). Also, neighborhood conditions may influence fruit removal (Manasse and Howe 1983; Sargent 1990), and may lead to differential mother plant fitness independent of individual traits. However, a variety of studies suggests that preferences of seed dispersers may in fact shape plant traits (Herrera 1981; Kalko et al. 1996; Korine et al. 2000; Schaefer 2002; Stanley et al. 2002; Schaefer et al. 2003; Schmidt and Schaefer 2004; Schmidt et al. 2004).

In the field, selection pressures can be demonstrated where visitation probability and fruit (or seed) removal by effective disperser species vary significantly with fruit traits and plant fruit display traits. Studies on bird-dispersed plants clearly dominate investigations of plant-frugivore relationships (e.g. Pratt and Stiles 1983; Davidar and Morton 1986; Denslow 1987; Foster 1990; Thébaud and Debussche 1992; Englund 1993; Willson and Whelan 1993, and citations above; Traveset 1994; Larson 1996; Herrera 1998), despite the fact that bats and monkeys are also important dispersers in tropical plant communities (Howe 1986; Jordano 2000). Here, we investigate fruit removal in a small, monkey-dispersed tree, *Leonia cymosa* (Violaceae), in the Amazonian rain forest of eastern Ecuador, focusing on the relationship of plant fruit display traits and fruit removal. We had identified tamarins as the main seed dispersers of *L. cymosa* in previous observations (see chapter 3.2). A separate analysis had revealed that tamarins did not respond to variation in fruit nutritional quality of focus trees (see chapter 4.1). The aims of this study were to clarify (1) whether there is evidence for selection of dispersers on fruit display traits of *L. cymosa*, (2) whether neighborhood conditions of an individual tree affect fruit removal, and (3) whether the hypothesis on the relation of fruit crop size and fruit removal, developed with main reference to bird-dispersed plants, is also valid for monkey-dispersed plants.

An important trait with respect to fruit removal and seed dispersal is the fruit crop size of a plant. The fruit crop size hypothesis (FCSH) states that feeding from a large fruit crop is more profitable than feeding from a small fruit crop because large crops allow frugivores to feed more economically, i.e. with less search effort and less moving (Howe and Estabrook 1977; Martin 1985). Therefore the FCSH predicts that plant individuals with large fruit crops are more attractive to frugivores, including dispersal agents, than those producing smaller fruit crops, with the former consequently having more seeds dispersed, in absolute numbers and relative to the effort spent in fruit production. Both effects would select for larger fruit crop sizes. However, such a tendency would be limited by the availability of dispersal agents. The FCSH has been corroborated by several studies of bird-dispersed plants (e.g. Davidar and Morton 1986; Denslow 1987; Sargent 1990). It has, however, not explicitly been tested for monkey-dispersed plants, although few data are available on how single monkey species exploit fruit trees. For example, Russo (2003) found that spider monkeys removed more fruits per visit when more ripe fruits were available in *Virola* trees, yet fruit crop size did not influence the proportion of the seed crop dispersed by spider monkeys during the entire fruiting season. Thus, fruit removal by these monkeys only in part followed the predictions of the FCSH. Here we evaluate the FCSH for *L. cymosa* and the monkeys feeding on its fruits.

We also considered other fruit display traits, as well as neighborhood conditions that may affect fruit removal. Tree size might influence fruit harvest by monkeys because rainforest animals have mostly clearly defined foraging heights (e.g. Ulloa 1988; Walther 2002). Moreover, the fruit ripening regime of a tree might play a role in determining fruit removal. As tamarins travel through their home ranges extensively (Boinski 1987; de la Torre 1991) and have a limited capacity of removing fruits during one visit (C. Knogge, personal communication and Knogge 1999) a constant fruit display throughout a long fruiting season may allow for a larger number of visits of tamarins than a peaked one, and should thus enhance dispersal. More fruits could be removed in trees fruiting desynchronized if intra-specific competition for dispersers exists. Furthermore, supply of fruits of the same species in the close neighborhood may either enhance fruit removal in trees forming part of tree groups, because frugivores having visited one tree might be attracted by resources of the same species visible from their current position. Yet, neighboring conspecific fruit supply may also result in reduced fruit removal from individual trees, because of competition for frugivores (cf. Manasse and Howe 1983). Finally, predation risk has to be integrated into resource selection decisions of frugivores (Martin 1985). Tamarins are prone to predation by forest raptors (Izawa 1978; Peres 1993; Vasquez and Heymann 2001), and may therefore avoid feeding in trees not well covered by neighboring vegetation.

4.2.2 Methods

Study site

Fieldwork was conducted in the evergreen tropical rain forest bordering Laguna Grande de Cuyabeno (0°2'N 76°15'W, elevation 250 m), located within the Cuyabeno Faunistic Reserve in north-eastern Ecuador. This area of Western-Amazonia has an annual precipitation of 3500 mm with a dry season from December to February and peak precipitations from April to June. A second but shorter dry period usually occurs in August and September. Annual mean temperature is 26 °C. The forest in the study area is characterized by a rich mosaic of terra firme, seasonally flooded plains of river borders and inner forest brooks, and swampy areas dominated by the morete palm (*Mauritia flexuosa*). Tree fall gaps are frequent. Forest canopy is at approx. 25 m. Old growth terra firme forest was shown to have a record breaking plant diversity (Valencia et al. 1994), non the less it is slightly disturbed by selective tree logging of the native population for the construction of large dugout canoes used locally. A forest-wide peak of fruit production occurs in this area from March to June (de Vries et al. 1993).

Study species and its frugivores

Leonia cymosa is an under storey tree occurring in the terra firme rain forest of western Amazonia near the Andes and of the Guyana shield (Missouri Botanical Garden 2009). In our study area, mean height of fruiting *L. cymosa* was 6.6 m (range: 2 m to 12.6 m, n = 306). It occurred at a density of 11.8 fruiting individuals per hectare (median from four plots of mapped trees with a total area of 21.6 ha). Trees tended to grow in clusters consisting of trees of different heights. *L. cymosa* bore fruits two times a year, in August/September and between March and May. Fruit ripening within trees expanded over these respective seasons. Ripe fruits of *Leonia* measured 13 to (rarely) 40 mm in diameter. Unripe *Leonia*-fruits were green turning pale yellow when ripe. Fruits contained 1 to 12 reniform seeds that range from 10 to 16 mm in length. The fruit pulp was sticky and tightly connected to the seed.

During the fruiting season of March to May 2000, we monitored fruit production and removal in 93 *L. cymosa* trees comprising the whole population of fruiting *L. cymosa* trees in two study plots of 5.5 hectare and of 6.5 hectare of old growth terra firme forest.

Black mantle tamarins, *Saguinus nigricollis* (Callitrichidae), and squirrel monkeys, *Saimiri sciureus* (Cebidae), and possibly an unknown nocturnal frugivore consumed the fruits of *L. cymosa* at our study site. Black mantle tamarins and squirrel monkeys differed widely in their effectiveness as seed dispersers. Black mantle tamarins swallowed the seeds together with the fruit pulp and defecated intact seeds far away from the mother tree. Squirrel monkeys opened the fruits while sitting in the *L. cymosa* tree to suck and gnaw on the fruit pulp, and then dropped seeds to the forest floor. Only occasionally they might have carried fruits to neighboring trees. Thus, fruit removal by tamarins almost completely accounted for seed dispersal whereas Squirrel monkeys did not disperse seeds, or at best in minimal numbers and small distances (see chapter 3.2).

Monkey sightings and observations in 2000 revealed that each of our study plots fell into the core home range of one group of tamarins (6-9 individuals per group), and of one group of squirrel monkeys (ca. 30 individuals per group) (see chapter 3.2). These group sizes as well as the spatial distribution of the groups were consistent with those from surveys carried out in the years before this study (1995-1997 unpublished data, and Müllner and Pfrommer 2001).

Data collection

Measuring fruit production and fruit removal

From end of March to May of 2000, we counted the complete standing crop of green and ripe fruits in the tree crowns weekly as well as the fallen fruits and peels on the ground below the trees, which allowed us to calculate the exact number of ripe fruits produced and removed per counting interval per individual tree. Beginning with the first sign of fruit removal by monkeys in any tree within the plots, trees were controlled every day from April 3rd of 2000 to May 10th of 2000. When peel remains indicated that fruits had been harvested by monkeys we counted the number of ripe fruits remaining in the crown.

We used different remains of feeding, and sightings of monkey groups shortly before tree controls to distinguish fruit consumption by tamarins from that by squirrel monkeys. Tamarins left behind large empty peel fragments, whereas squirrel monkeys left behind numerous comparatively small peel fragments together with many separated seeds scattered over the ground below trees. Such seeds showed a rough-textured surface. Using these traces, 93% of the feeding events (n = 200) could be unequivocally assigned to each monkey species without direct observation. We had difficulties only in categorizing 14 feeding events, with a total of 56 fruits consumed (= 2% of all fruits removed by monkeys). These difficulties arose from finding peel fragments of only intermediate size, or seeds without clear gnawing marks. In these cases we assigned the fruits removed from a tree to squirrel monkeys if the tree belonged to a patch where these had removed large amounts of fruits. This is reasonable because groups of squirrel monkeys are much large than tamarin groups and are usually distributed over a whole patch of trees while traveling and feeding. We assigned the fruits removed from a tree with ambiguous feeding remains to tamarins if there were no traces of a visit of squirrel monkeys in the plot at that day, and also if such a tree stood more than 30 m away from a patch of trees with feeding traces of squirrel monkeys. ArcView-maps of fruit consumption for each control day were used analyzing the spatial pattern of feeding events.

We calculated a seasonal fruit crop size for every tree by summing up the ripe fruits it produced during all count intervals. Likewise, we calculated the total number of fruits removed from each tree by tamarins and squirrel monkeys, respectively, by summing up the respective values from the count intervals.

Measuring tree and fruit display traits and neighborhood conditions

Tree height at the highest point of the crown was measured by help of a relascope (FOB, Salzburg, Austria). The synchrony of fruit maturation of a tree with conspecifics was expressed as the time deviation of its peak of fruit maturation from the median peak of fruit maturation of all trees monitored (in days). We defined the individual peak of fruit maturation of a tree as the date when the cumulative number of fruits that had matured in the tree had reached or just exceeded half of the total seasonal fruit crop size. Thus, a negative deviation from the sample median indicates that a tree fruited earlier than the population wide peak of fruiting, whereas a positive value of deviation indicates that its fruit production peaked later. As a measure to characterize the evenness or constancy of fruit production of an individual during the time of observation we calculated the coefficient of variation (CV = sd/mean) of the number of fruits produced per counting interval, including the first count. We only included trees in our analysis that produced a number of fruits equal or bigger than the number of counting intervals (6 fruits).

Predation risk was quantified by estimating the percentage of the total peripheral area of the tree crown remaining uncovered by neighboring vegetation. A value of 100% indicates that a tree crown stood completely in an open space. The other extreme of 0% signifies that a tree crown was embedded in foliage and branches of other trees or lianas coming close to it from all sides. The conspecific fruit production in the neighborhood of a *L. cymosa* was quantified as the sum of all ripe fruits produced throughout the fruiting season within a radius of 15 m. We defined "neighborhood" this way, because trials with 60 trees in 1999 had shown that we were able to locate conspecific trees by sight from tree crown to tree crown to a maximum distance of 15 m. We assumed that monkeys are capable to do the same.

Statistical analysis

We used Generalized Linear Models (GLMs) to identify effects of fruit display traits both on the probability of a *L. cymosa* tree to be harvested by the respective monkey species (the first component of fruit removal), as well as on the number of fruits removed, and the percentage of fruits removed by the respective monkey species (the second component of fruit removal). Subsequently, we tested for correlations of the regression model residuals with the neighborhood variable "percent uncovered", and we tested for spatial correlations of the residuals in order to find competition or enhancement effects of conspecific neighboring fruit offer. Thus, we examined to what extent variation unexplained by tree traits could be explained by neighborhood conditions. By this two step technique we avoided to overcharge regression models with variables and acknowledged the different nature of the variables (tree fruit display traits vs. spatial position).

All GLMs and correlations were calculated with the Statistical package R 1.8.1 (R Development Core Team 2003). We categorized the individual *L. cymosa* tree as having been found and harvested by monkeys if at least one event of fruit removal could be observed in this tree throughout the fruiting season. We used GLMs with binomial errors for the binary response variable (equivalent to a logistic regression) to analyze the probability of harvest. Models were simplified by stepwise backward elimination of the variable with the smallest AIC-Values (Crawley 2002).

Only trees harvested at least once by either of the two species were included in the analysis of the number and the percentage of fruits removed. To analyze the number of fruits removed we fitted GLMs with quasipoisson errors for count data. The GLM-procedures quasipoisson (log link function) was chosen to account for overdispersion. The percentage of fruits removed was analyzed by means of a weighted regression, using the individual sample sizes (i.e. the total seasonal fruit production) as weights, and the logit link function to ensure linearity (Crawley 2002, p. 513 ff). We chose a weighted regression to avoid that a proportion from a tiny sample (e.g. 5 fruits removed out of 10 fruits produced) gave an undue influence on the slope of the regression. A weighted regression is performed in R by a GLM with binomial errors that works with a response vector containing the number of fruits taken away and the number of fruits left (the number of successes as well as the number of failures) instead of the proportion values (%). This GLM gives low weight to estimates with small individual sample sizes (= small binomial denominators). The GLM – procedure "quasibinomial" was chosen to account for overdispersion. Models of this part of the analysis were simplified by manual stepwise backward elimination of variables with subsequent ANOVAs and F-tests as described in (Crawley 2002). As a measure of variation explained by GLMs, equivalent to the coefficient of determination (r^2) in a linear model, we calculated the ratio deviance change / null deviance (deviance change = null deviance – residual deviance). We used Spearman rank correlations to test for correlations of the regression model residuals with the variable "percent uncovered".

For the purpose of examining the influence of conspecific fruit production in the neighborhood on fruit removal, we analyzed the spatial pattern of the residuals from the GLMs. If spatial dependence existed, residuals should be locally alike. As negative residuals mean that removal in trees was lower than expected by the model, clusters of negative residuals are an indication for competition for frugivores within a group of trees, or failure to attract visitors. Clusters of positive residuals, on the other hand, indicate an enhancement of fruit harvest in fruit patches of several neighboring trees. Spatial dependence of the residuals was examined by Mantel tests run with Euclidean distance matrices of residuals and of Euclidean distance of the tree's positions, derived from a GIS-map. We used the extension "Distance matrix, v 1.4" for ArcView GIS 3.2 (Jenness 2004) to calculate distance matrices for respective tree samples, and the program PcOrd 4.0 (McCune and Mefford 1999) to run the Mantel tests. The significance of correlation was determined by means of a Monte Carlo randomization test with the Mantel's (Z) values from 9999 permutations. A positive correlation of tree distances and residuals, indicated by a positive Mantel's (r), means that the closer trees stand to each other, the more similar are the residuals from a regression model. Since the calculation of Euclidean distances results in positive values only, the results of a Mantel test can not be directly interpreted in the context of enhancement (positive residuals at close spatial position) versus competition (negative residuals; see above). However, a small distance of residuals in a tree pair can only result from either two positive or two negative residuals. Therefore, in case of a significant, positive Mantel's (r), the effect of neighborhood conspecific fruit abundance conditions can be visualized by plotting the residuals against the number of *L. cymosa* fruits within a radius of 15 m.

4.2.3 Results

Characterization of fruit production and consumption by monkeys

Median productivity of the trees was 36 ripe fruits throughout the whole fruiting season. The maximum of ripe fruits produced per season by a single tree was 427. 75% of the trees had standing crops of only up to 30 ripe fruits. The maximum standing crop of fruits in a tree was 324 fruits. Seasonal fruit production was not significantly correlated with tree size (Spearman R = 0.185, p = 0.08, n = 92).

55% of all feeding visits recorded in *L. cymosa* trees were by tamarins, whereas 45% were by squirrel monkeys. Tamarins visited the study plots more frequently than squirrel monkeys (e.g. mean interval between harvests of 1.8 days versus 4.3 days in one plot). Per visit in a plot, tamarins fed on fewer trees than squirrel monkeys (e.g. mean number of trees exploited per visit of 3.2 versus 7.8 in one plot). In a single tree, tamarins harvested from 1 to 25 fruits per visit, while squirrel monkeys harvested from 1 to 224 fruits per visit. Both monkey species left ripe fruits behind in the tree crowns in 97% of all feeding events.

Probability of fruit removal

The probability of fruit removal by tamarins, as well as by squirrel monkeys increased significantly with the seasonal fruit crop size of *L. cymosa* - trees (Table 1). Yet, with increasing tree height, squirrel monkeys removed fruits with a significantly lower probability.

Tamarins harvested *L. cymosa* trees less likely the more open these stood in the understorey, as indicated by the significantly negative correlation of the residuals from the GLM for the probability of fruit removal by tamarins with the variable “percent uncovered by surrounding vegetation” (n = 86, Spearman R = -0.27, p = 0.013).

The smallest seasonal fruit crop sizes (of 6-10 fruits) had a 45% chance to have fruits removed by tamarins, a 50% chance to have fruits removed by squirrel monkeys. The probability of fruit removal by tamarins rose more slowly with increasing fruit crop size than that of fruit removal by squirrel monkeys (Figure 1), indicating that tamarins respond differently to fruit crop size at the initial step of fruit removal. The effect of seasonal fruit crop size on the probability of fruit removal by tamarins leveled off at 200 – 250 ripe fruits. We did not find any spatial correlations of residuals of the logistic regression models (see statistics in Table 2). Therefore, the probability of fruit harvest by tamarins in a focus tree was neither enhanced nor reduced by the amount of fruits offered by other *Leonia* trees in its neighborhood.

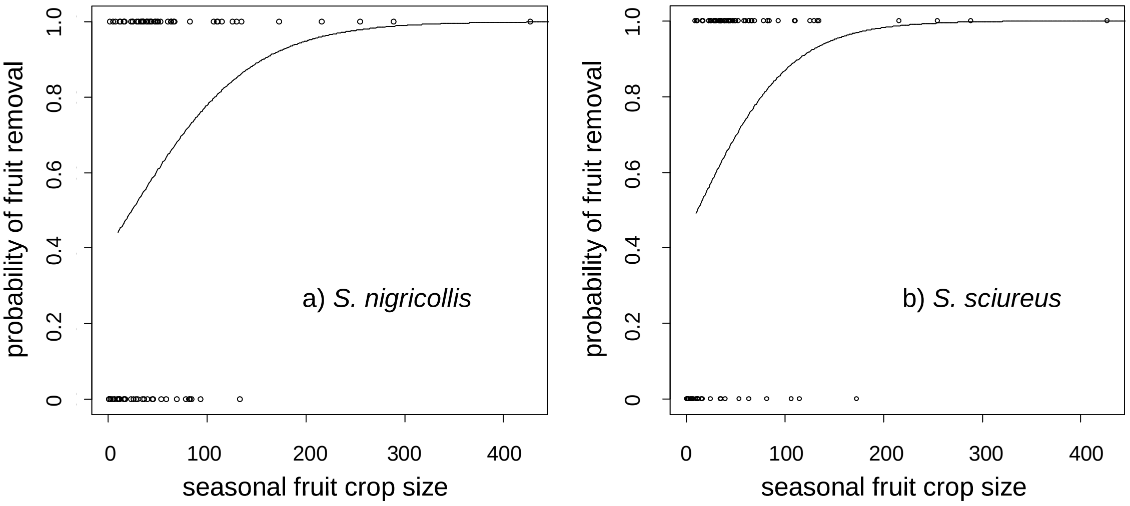

Figure 1. Logistic regression of the relationship between seasonal fruit crop size and the probability of fruit removal in *L. cymosa* trees by a) black mantle tamarins, *Saguinus nigricollis*, and b) squirrel monkeys, *Saimiri sciureus* at Laguna Grande de Cuyabeno, Ecuador.

Table1. Influence of predictor variables on the probability of fruit removal**,** the number of fruits removed, and the proportion of fruits removed from trees of *L. cymosa* by black mantle tamarins, *Saguinus nigricollis,* and by squirrel monkeys, *Saimiri sciureus,* at Laguna Grande de Cuyabeno, Ecuador. Results from regression models with tree traits and subsequent Spearman rank correlation of model residuals with tree covering. **+** indicates positive correlation, **-** indicates negative correlation. For model summaries see Appendix F.

GLM	Probability of fruit removal by *Saguinus*	Probability of fruit removal by *Saimiri*	Number of fruits removed by *Saguinus*	Number of fruits removed by *Saimiri*	Proportion of fruits removed by *Saguinus*	Proportion of fruits removed by *Saimiri*
N	86	86	49	57	49	57
Seasonal fruit crop size	+ *	+ **	+ ***	+ ***	- *	+ ***
Tree height		- *				
Synchrony of fruiting (deviation from sample median)				- **		
Individual fruiting pattern (CV of fruit production)						
Variation explained (%)	8	17	20	82	13	38
Variation explained by crop size alone (%)		10		79		
Spearman Rank Correlation	Residuals					
Percent uncovered by surrounding vegetation	- #					

Significance level of coefficients: * $p<0.05$, ** $p<0.01$, ***$p<0.001$

Significance level of Spearman rank correlation: # $p<0.05$

Number of fruits removed

The number of fruits removed from an individual tree by tamarins, as well as by squirrel monkeys, increased significantly with increasing seasonal fruit crop size (Table 1). Moreover, squirrel monkeys removed significantly fewer fruits in trees with an individual fruiting peak later than the median fruiting peak of all trees observed. This effect of an individual fruit production peak late in the fruiting season was small in small fruit crops and prominent in large fruit crops (Figure 2 c; note that GLMs for Poisson distributed errors fit a logarithmic growth to the variables of the model, and thus it is possible that the predicted values exceed the range of the input variable). Still, including the synchrony of fruiting into the model caused only a small, though significant change in deviance and thus in variation explained by the model.

The residuals of the GLMs having the number of fruits as dependent variable did not correlate significantly with the degree of covering of trees by surrounding vegetation. No significant spatial correlations of model residuals were found (Table 2). Thus, the number of fruits removed, too, was neither enhanced nor reduced by the amount of fruits offered by other *L. cymosa* trees in its neighborhood.

Proportion of fruits removed

With growing seasonal fruit crop size of *L. cymosa* trees, tamarins removed a significantly decreasing proportion of fruits, while for squirrel monkeys the opposite was found (Table 1, Figures 2 b and d). All GLMs with the proportion of fruits removed as dependent variable explained less of the variation than those with the absolute number of fruits removed.

For both monkeys, we found significant positive spatial correlations of the residuals of the GLMs having the proportion of fruits removed as dependent variable (Table 2, and statistics therein). These spatial correlations indicate an effect of the abundance of conspecific fruits in the neighborhood of a tree on the removal of its fruits (Figure 3). Large numbers of conspecific fruits in the neighborhood of a *L. cymosa* tree led to lower proportions of fruits removed by tamarins than expected by the model, indicating that increasing conspecific fruit abundance had the effect of reducing the proportion of fruits removed from a tree by them. On the other hand, large numbers of conspecific fruits in the neighborhood led to higher proportions of fruits removed by squirrel monkeys than expected by the model, indicating that increasing conspecific fruit supply in the neighborhood enhanced the proportion of fruits removed from a *L. cymosa* tree by squirrel monkeys.

Figure 2. The relationship between seasonal fruit crop size and the number of fruits, as well as the proportion of fruits harvested throughout the fruiting season as predicted by GLMs. a) Number of fruits, and b) proportion of fruits harvested by black mantle tamarins, *Saguinus nigricollis*. c) Number of fruits, and d) proportion of fruits harvested by squirrel monkeys *Saimiri sciureus,* at Laguna Grande de Cuyabeno, Ecuador.

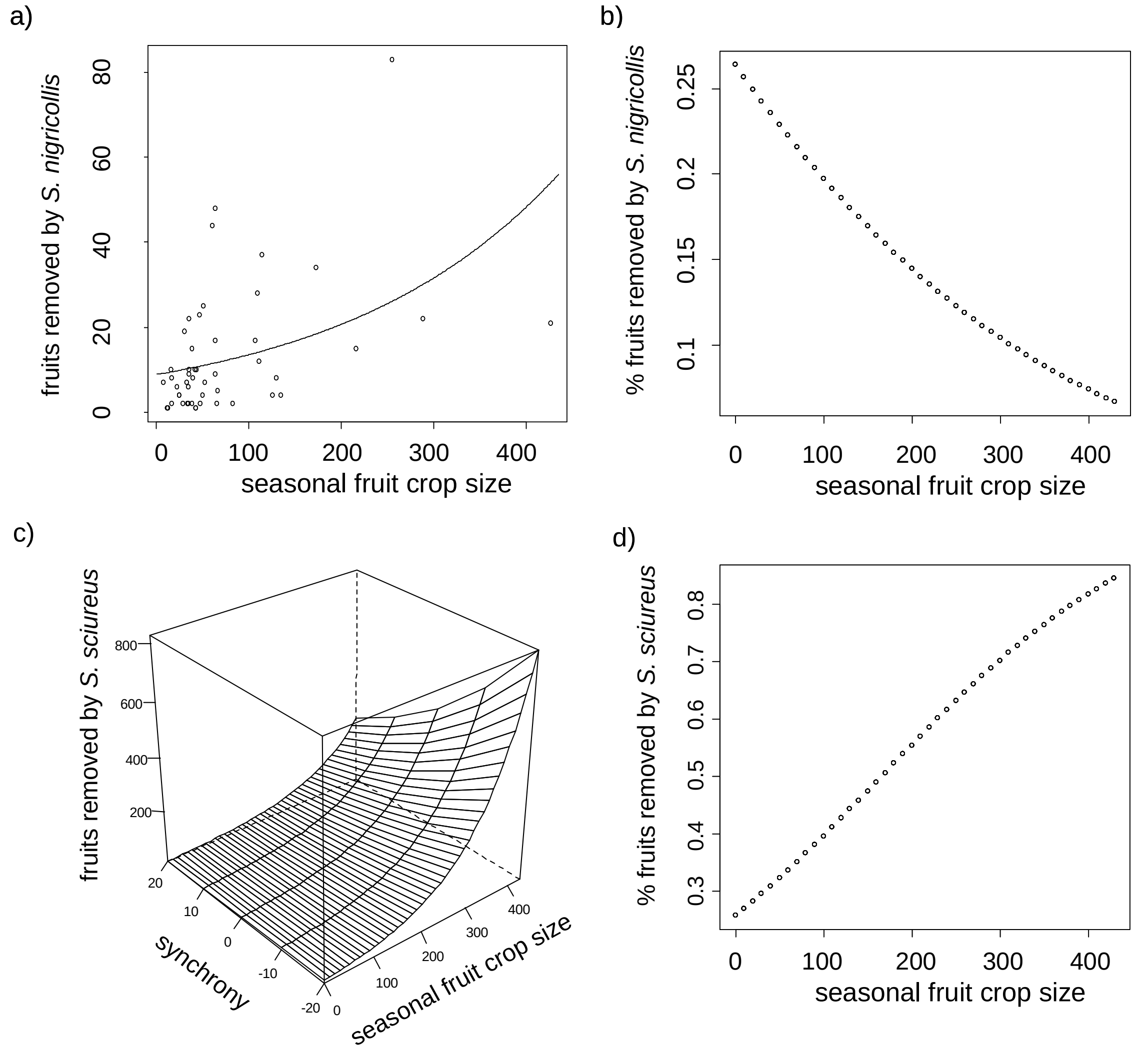

Table 2. Analysis of spatial dependence of residuals from regression models of the probability of fruit removal**,** the number, and the proportion of fruits removed from trees of *L. cymosa* by black mantle tamarins*, Saguinus nigricollis,* and by squirrel monkeys, *Saimiri sciureus,* at Laguna Grande de Cuyabeno, Ecuador. Results from Mantel tests for association of tree position and residuals from regression models, each test based on a tree distance matrix and a Euclidean distance matrix of residuals. r = standardized Mantel statistic, Randomization test with 9999 permutations. Size = matrix size, number of cells/rows. lr = logistic regression, mr = multiple regression

Model	Dependant variable	Size	r	p
lr	Probability of fruit removal (0/1) by tamarins	86	0.024	0.085
lr	Probability of fruit removal (0/1) by squirrel monkeys	86	0.013	0.161
mr	Number of fruits removed by tamarins	51	0.063	0.121
mr	Number of fruits removed by squirrel monkeys	57	0.022	0.142
mr	Proportion of fruits removed by tamarins	51	0.123	0.024
mr	Proportion of fruits removed by squirrel monkeys	57	0.052	0.033

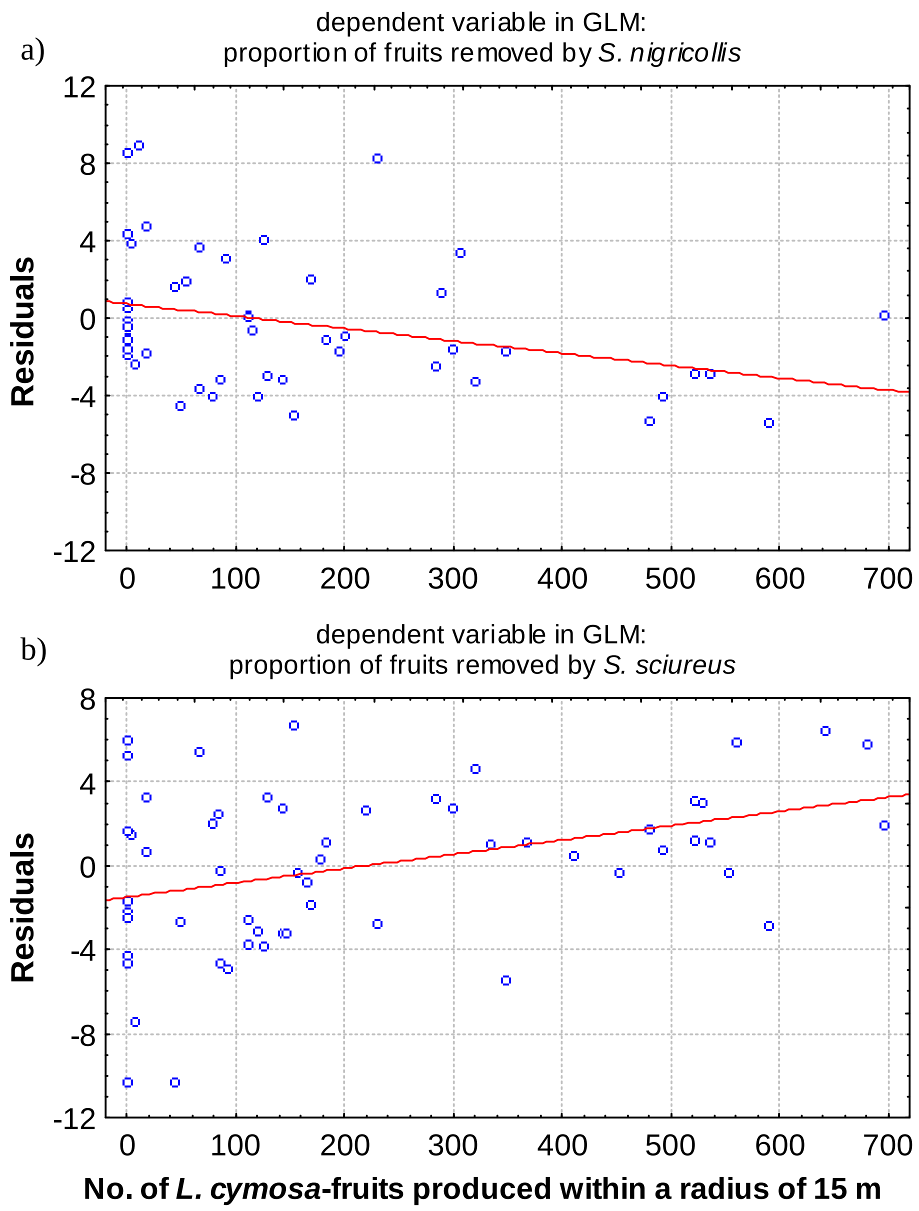

Figure 3. Effect of conspecific fruit abundance in the neighbourhood on the proportion of fruits removed from trees of *L. cymosa* at Laguna Grande de Cuyabeno. Residuals from the respective GLMs with the proportion of fruits removed (a) by black mantle tamarins, *Saguinus nigricollis*, and (b) by squirrel monkeys, *Saimiri sciureus*, plotted against the total seasonal fruit production within a diameter of 15 m around each tree. Based on significant spatial correlations of residuals (see Table 2 with results from Mantel tests).

4.2.4 Discussion

Consequences of fruit removal by the disperser

L. cymosa trees with larger seasonal fruit crop size had a larger number of fruits removed by black mantle tamarins, the effective and reliable seed dispersers, i.e. a higher dispersal success. They also had a higher probability to have fruits removed by the disperser than those with small seasonal fruit crop sizes. Consistent with the fruit crop size hypothesis (FCSH), these results show that tamarins exert a selective pressure on seasonal fruit crop sizes to increase. However, the proportion of fruits removed by the disperser, i.e. the dispersal efficiency of an individual *L. cymosa* tree, decreased with increasing seasonal fruit crop size. Again in accordance with the FCSH, this may limit fruit crop sizes, because energy allocated into too many undispersed seeds is wasted. Furthermore, the proportion of fruits removed by tamarins is reduced in *L. cymosa* -trees with high conspecific fruit abundance in their neighborhood. This finding suggests competition of individual trees for the disperser (likewise in Manasse and Howe 1983; Denslow 1987), and thus fulfils a basic assumption of the FCSH (Howe and Estabrook 1977).

In our study site, the median seasonal fruit crops size of *L. cymosa* was only 36 ripe fruits and productivity was not correlated with tree size (see chapter 3.1). The observed relationship of fruit removal by tamarins with seasonal fruit crop sizes suggests that the latter may indeed result from selective pressures exerted by the disperser.

Our findings provide new evidence that FCSH applies also to a monkey-dispersed plant, as far as the predicted relations of fruit production and fruit removal are concerned. Yet, in the dispersal system of *L. cymosa*, the mechanisms leading to the selective pressure on fruit crop size are different from those proposed in the FCSH. The FCSH assumes that feeding profitability is the major factor that makes large fruit crop sizes more attractive to frugivores than small fruit crop sizes. This does not hold true for the disperser of *L. cymosa* in our study site. Tamarins swallowed seeds together with the fruit pulp and removed only few fruits per visit. These observations are supported by studies of other species of *Saguinus*, where the food uptake per tree visit was also limited to few fruits, especially when tamarins swallowed large seeds (C. Knogge, personal communication; Knogge 1999; Knogge and Heymann 2003). Thus, large fruit crops do not allow the individual disperser to take up more food per visit in *L. cymosa*. Although feeding in large fruit crops is not more profitable for the individual tamarin, large fruit crop sizes are still advantageous because they should make the fruit display more visible and thus should raise the probability to be detected by tamarins. Large fruit crop sizes may be also attractive to tamarins because they may offer more choice of fruits within the tree. Furthermore, large fruit crops of *L. cymosa* allow more individuals of the tamarin group to feed during the same visit, and to remove more fruits at repeated visits. Therefore, the dispersal success of a tree increased with seasonal fruit crop size. However, the dispersal efficiency of a tree, i.e. the proportion of fruits tamarins removed throughout the season, did not increase with fruit production, because of the low fruit removal capacity and availability of the tamarins. Considering the fact that the trees in our study plots were regularly visited by only one group of tamarins with 6-9 individuals, respectively, the dispersal system of *L. cymosa* presents a case of extremely limited disperser availability.

Fruit removal by tamarins was neither significantly predicted by the synchrony of fruiting of the individual tree with the population nor by the fruit ripening pattern of individual trees. All trees seemed to have offered ripe fruits for a time sufficiently long to ensure fruit harvest by tamarins.

Our findings are most comparable to the results of a study of three bird-dispersed plant species of the tropical cloud-forest understorey in Costa Rica, reported by Murray (1987). Their fruits are removed by only three bird species, while in many other bird dispersed plants the number of dispersing species is much higher (e.g. 24 species in *Viburnum dentatum* (Caprifoliaceae), Sargent, 1990). Similar to our results in *Leonia*, the probability of visitation of the cloud forest under storey plants increased with increasing crop size. Among visited individuals the number of fruits removed per day increased with crop size, too, while the proportion of fruits removed decreased. Failure of several other studies of bird-dispersed plants with larger bird assemblages to find full support for all components of the FCSH (Davidar and Morton 1986; Denslow 1987; Willson 1988; Carr 1992; French et al. 1992; Willson and Whelan 1993) may have resulted from not having sufficiently differentiated between responses to fruit crop size of the various bird species involved, which may differ rather strongly from each other in their foraging behavior and removal capacities.

As hypothesized, black mantle tamarins harvested *L. cymosa* trees less likely that were not or less completely covered by surrounding vegetation, although these trees and their fruits should have been more visible from a distance. Sit-and-wait hunting forest raptors represent an important predatory threat to tamarins (Izawa 1978). Peres (1993) observed one raptor attack every nine days on a mixed species *Saguinus*-group in the Urucu River, Central Amazonia, Brazil. In order to protect themselves, tamarins show complex vigilance behavior (Heymann 1990), however, forest raptors are able to overcome this by their surprise hunting tactics, especially in the canopy and in open spaces within the forest (Vasquez and Heymann 2001). Tamarins might well try to avoid predation by staying away from hard-to-judge risk, like a *L. cymosa* tree that allows free aerial access from the surrounding sub canopy.

Although our results suggest selection of the disperser on fruit display traits of *L. cymosa*, they also show that some factors, such as predation risk at a particular site, may constrain selective pressures. Another constraint on selection by dispersers on fruit display traits is the competition among individual *L. cymosa* trees for dispersal agents occurring in a neighborhood of high conspecific tree density. Such competition is a precondition for the FCSH, but it may also limit selection because the neighborhood conditions that are out of control of the individual may override the effect of individual fruit display traits.

Consequences of fruit removal by the non-disperser

The probability of fruit removal, the number of fruits removed, and the proportion of fruits removed by squirrel monkeys increased significantly with seasonal fruit crop sizes. Thus, fruit removal by squirrel monkeys, the non-dispersing fruit users of *L. cymosa*, supported the assumptions of FCSH more strongly than fruit removal by tamarins. The main reason for this is the different way squirrel monkeys consumed fruits of *L. cymosa* together with the large group size of squirrel monkeys of approximately 30 individuals. In contrast to tamarins, squirrel monkeys spat out seeds, which allowed individuals to harvest larger amounts of fruits per visit. Thus, these monkeys could take advantage of large temporary fruit offers going hand in hand with large seasonal fruit crop sizes, and therefore highly productive trees may indeed be more attractive to individual squirrel monkeys. This could explain the faster response in the probability of harvest of squirrel monkeys to increasing seasonal fruit crop size, as compared to tamarins, and the disproportionately high fruit removal from large seasonal fruit crops by this species. It is more difficult to explain the enhanced proportion of fruits removed by squirrel monkeys in *L. cymosa* trees with high conspecific fruit abundance in their neighborhood. We can only assume that squirrel monkey groups suspend traveling when encountering a patch of trees with ripe fruits, resulting in higher fruit consumption during the visit, as compared to the fruit consumption in single trees exploited while the group is traveling. More behavioral observations of the foraging behavior of squirrel monkeys would be needed to verify this assumption.

The significant variation in fruit removal by squirrel monkeys with seasonal fruit crop sizes of *L. cymosa* renders it possible that this non-disperser as well exerts selection pressure on fruit crop sizes of this tree. This may be the case if squirrel monkeys remove more than the surplus of fruits not used by tamarins, yet produced with respect to attract visits of the disperser. This should result in a selection pressure against large seasonal fruit crop sizes, to limit the attraction to squirrel monkeys. Furthermore, it should result in a selection pressure on the fruit display to extend over longer periods of time, thus reducing the risk to loose a large proportion of the fruits to the non-disperser. Previous studies have interpreted temporally expanded fruit displays as a strategy to avoid rapid satiation of relatively rare seed-dispersers (Howe and Estabrook 1977). Likewise, the prolonged fruit display observed in *L. cymosa* may be seen as a strategy to avoid losses of fruits to squirrel monkeys.

Another potential way to reduce fruit losses to the non-disperser may be fruiting late, as demonstrated by our finding that squirrel monkeys removed significantly lower numbers of fruits from *L. cymosa* trees whose fruit production occurred later than the median fruiting peak of all trees observed. The effect of late fruiting was stronger in large fruit crops, compared to small fruit crops, because of the disproportionately high fruit removal by squirrel monkeys in large seasonal fruit crops. We observed that squirrel monkeys harvested only few fruits of *L. cymosa* in the last third of its fruiting season (see chapter 3.2). At that time the general fruit availability in the forest might have increased, because at forest transects near our study plots de Vries et al. (1993) have determined a consistent peak of fruiting tree species from May to July in two consecutive years. Therefore it is possible that towards the end of the *L. cymosa* fruiting season in 2000 other (fruit) resources became available to squirrel monkeys that ranked higher in their preference.

The finding that squirrel monkeys harvested large *L. cymosa* trees less likely is difficult to explain, given that Ulloa (1988) reported heights of 3-15 m as the most used forest stratum by this species in our study area, which is the height range all tree crowns of *L. cymosa* in the current study fell into. Ulloa did not specify different activities within this range. As we have no own data on forest stratum use of squirrel monkeys, and as we could not find more detailed data in the literature, we can only speculate that squirrel monkeys might travel through the inner forest at low heights. As a consequence, they might avoid large *L. cymosa* trees more frequently than small and mean sized trees.

In contrast to tamarins, squirrel monkeys were not deterred by open spaces in the sub-canopy, probably for two reasons: first, they are heavier than tamarins, and thus are less prone to predation by mid-sized raptors. Second, their groups are larger, which may result in a higher vigilance and a better ability to detect raptors.

Conclusions

Our results indicate that the FCSH is applicable to a broad range of dispersal systems, as long as the specific foraging behavior of the respective seed dispersers is being considered. Different responses of frugivores to fruit offers based on different foraging behavior, morphology, and physiology may lead to the same selection pressures on fruit crop size.

Opposed to the view that contrasting responses of frugivores to fruit and fruit display traits lead to inconsistent selection, this study showed that in the same plant seed dispersers and other frugivores not dispersing seeds may exert concordant selection pressures. Factors beyond the control of individual trees may constrain, yet not impede selection on fruit display traits.

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References

Boinski, S. (1987). Habitat use by squirrel monkeys (*Saimiri oerstedi*) in Costa Rica. Folia Primatologica 49: 151-167.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of Populations, Proceedings of the Advanced Study Institute on 'Dynamics of Numbers in Populations', Oosterbeek, NL, 7-18 September 1970. P. J. den Boer and G. R. Gradwell. Wageningen, Centre for Agricultural Publishing and Documentation: 298-312.

Crawley, M. J. (2002). Statistical computing: an introduction to data analysis using S-Plus. Chichester, Wiley.

Davidar, P. and E. S. Morton (1986). The relationship between fruit crop sizes and fruit removal rates by birds. Ecology 67: 262-265.

de la Torre, S. (1991) Area de vida, comportamiento reproductivo y habitat de *Saguinus nigricollis graellsi* (Primates: Callitrichidae) en la Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 162

de Vries, T., F. Campos, S. de la Torre, E. Asanza, A. C. Sosa and F. Rodriguez (1993). Investigación y conservación en la Reserva de Producción Faunistica Cuyabeno. La investigación para la conservación de la diversidad biológica en el Ecuador. Memorias del simposio llevado a cabo del 10 al 12 de junio de 1992, Quito, Ecosciencia.

Denslow, J. S. (1987). Fruit removal rates from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. Canadian Journal of Botany 65: 1299-1235.

Englund, R. (1993). Fruit removal in *Viburnum opulus*: copius seed predation and sporadic massive seed dispersal in a temperate shrub. Oikos 67: 503-510.

Foster, M. S. (1990). Factors influencing bird foraging preferences among conspecific fruit-trees. Condor 92: 844-854.

Harms, K. E., S. J. Wright, O. Calderón, A. Hernández and E. A. Herre (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404: 493-495.

Herrera, C. M. (1981). Fruit Variation and Competition for Dispersers in Natural Populations of *Smilax aspera*. Oikos 36: 51-58.

Herrera, C. M. (1985). Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132-141.

Herrera, C. M. (1998). Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: A 12-year study. Ecological Monographs 68: 511-538.

Heymann, E. W. (1990). Reactions of wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. International Journal of Primatology 11: 327-337.

Howe, H. F. (1986). Seed dispersal by fruit-eating birds and mammals. Seed dispersal. D. R. Murray, Academic Press, Australia: 123-189.

Howe, H. F. and G. F. Estabrook (1977). On intraspecific competition for avian dispersers in tropical trees. American Naturalist 111: 817-832.

Howe, H. F. and J. Smallwood (1982). Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13: 201-228.

Izawa, K. (1978). A field study on the ecology and behavior of the Black-mantle tamarin (*Saguinus nigricollis*). Primates 19: 241-274.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501-521.

Jenness, J. (2004). Distance Matrix (dist_mat_jen.avx) extension for ArcView 3.x, v. 1.4. Flagstaff, Arizona, U.S.A., Jenness Enterprises. Available at: http://www.jennessent.com/arcview/dist_matrix.htm.

Jordano, P. (2000). Fruits and frugivory. Seeds - the ecology of regeneration of plant communities. M. Fenner, Chapman and Hall.

Kalko, E. K. V., E. A. Herre and C. O. Handley (1996). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. Journal of Biogeography 23: 565-576.

Knogge, C. (1999). Tier-Pflanze-Interaktion im Amazonas-Regenwald: Samenausbreitung durch die sympatrischen Tamarinarten *Saguinus mystax* und *Saguinus fuscicollis* (Callitrichidae, Primates). Münster, Schüling Verlag: 151.

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.

Korine, C., E. K. V. Kalko and E. A. Herre (2000). Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. Oecologia 123: 560-568.

Larson, D. L. (1996). Seed dispersal by specialist versus generalist foragers: the plant's perspective. Oikos 76: 113-120.

Manasse, R. M. and H. F. Howe (1983). Competition for dispersal agents among tropical trees: influences of neighbors. Oecologia 59: 185-190.

Martin, T. E. (1985). Resource selection by tropical frugivorous birds: integrating multiple interactions. Oecologia 66: 563-573.

McCune, B. and M. J. Mefford (1999). PC-Ord: Multivarate Analysis of Ecological Data, Version 4.0. Gleneden Beach, Oregon, U.S.A., MjM Software.

Missouri Botanical Garden (2009). w3TROPICOS. Searched item: *Leonia cymosa*. 09.02.2009. Data base. Missouri Botanical Garden, St. Louis, Missouri.

Müllner, A. and A. Pfrommer (2001). Regenwaldtourismus und sein Einfluss auf ausgewählte Wildtierarten am Río Cuyabeno. Roßdorf, TZ-Verlagsgesellschaft mbH.

Murray, K. G. (1987). Selection for optimal fruit-crop size in bird-dispersed plants. The American Naturalist 129: 18-31.

Peres, C. A. (1993). Anti-Predation Benefits in a Mixed-Species Group of Amazonian Tamarins. Folia Primatologica 61: 61-76.

Pratt, T. K. and E. W. Stiles (1983). How long fruit-eating birds stay in the plants where they feed: Implications for seed dispersal. The American Naturalist 122: 797-805.

R Development Core Team (2003). R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing, URL http://www.R-project.org. Version 1.8.1.

Russo, S. E. (2003). Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. Oecologia 136: 80-87.

Sargent, S. (1990). Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). Ecology 71: 1289-1298.

Schaefer, H.M. (2002) The influence of fruit pulp chemistry on avian fruit choice. Dissertation, Fachbereich Biologie, Geo- und Umweltwissenschaften, Universität Oldenburg, Oldenburg, pp 114

Schaefer, H. M., V. Schmidt and H. Winkler (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. Oikos 102: 318-328.

Schmidt, V. and H. M. Schaefer (2004). Unlearned preference for red may facilitate recognition of palatable food in young omnivorous birds. Evolutionary Ecology Research 6: 919-925.

Schmidt, V., H. M. Schaefer and H. Winkler (2004). Conspicuousness, not colour as foraging cue in plant-animal signalling. Oikos 106: 551-557.

Stanley, M. C., E. Smallwood and A. Lill (2002). The response of captive silvereyes (*Zosterops lateralis*) to the colour and size of fruit. Australian Journal of Zoology 50: 205-213.

Thébaud, C. and M. Debussche (1992). A field test of the effects of infructescens size on fruit removal by bird in *Vibirnum tinus*. Oikos 65: 391-394.

Traveset, A. (1994). Influence of type of avian frugivory on the fitness of *Pistacia terebinthus* L. Evolutionary Ecology 8: 618-627.

Ulloa, R. (1988) Estudio sinecologico de primates en la Reserva de Producción Faunistica Cuyabeno, Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 179

Valencia, R., H. Balslev and G. Paz y Mino (1994). High tree alpha-diversity in Amazonian Ecuador. Biodiversity and Conservation 3: 21-28.

Vasquez, M. R. O. and E. W. Heymann (2001). Crested Eagle (*Morphnus guianensis*) Predation on Infant Tamarin (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichinae). Folia Primatologica 72: 301–303.

Walther, B. A. (2002). Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. Journal für Ornithologie 143: 64-81.

Wang, B. C. and T. B. Smith (2002). Closing the seed dispersal loop. Trends in Ecology and Evolution 117: 379-385.

Wheelwright, N. and G. Orians (1982). Seed dispersal by animals - contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist 119: 402-413.

Willson, M. F. and C. J. Whelan (1993). Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. Ecological Monographs 63: 151-172.

5 Synopsis

The dominance of trees with fleshy fruits that nourish a wide range of frugivorous animals is one of the most prominent features of many tropical rain forests all over the world (Howe and Smallwood 1982; Jordano 2000). The importance of fruits as a food resource becomes especially apparent upon observing the weight loss of frugivores in times of fruit scarcity (e.g. in Bornean orangutans, Knott 1998). Frugivores, on the other hand, are of outstanding importance for seed dispersal. A loss of frugivore species diversity is expected to result in reduced plant diversity (Chapman and Onderdonk 1998; Webb and Peart 2001). The mutual interdependence of plants and “their” frugivores supposes a very close interaction. van der Pijl (1969) was one of the first to approach the interaction in a systematic way. He defined so-called fruit syndromes, which describe constellations of fruit traits matching with certain frugivores’ needs and capacities. Shortly thereafter, the crucial role of seed dispersal in the plant reproductive cycle and the density-dependent mortality of seeds as an ecological mechanism to maintain species diversity were recognized by Janzen (1970) and Connell (1971) (and eventually confirmed by Harms et al. 2000).

As a fundamental process, animal seed dispersal received great attention, focusing on the question of how the supposedly close fruit and frugivore interactions may have evolved. At first, the relationship between plants and frugivores was characterized as a result of co-evolution (Snow 1971; McKey 1975). However, it soon became clear that the requirements for a co-evolutionary process were not met in fruiting plant-frugivore interactions: species to species relationships could not be found and plants have little control over the service of frugivores, because they offer the reward for a potential dispersal in advance. Also, there are often many different species of fruit users in one tree that treat fruits and seeds differently (Wheelwright and Orians 1982; Herrera 1985). As a result, the interaction was (and is currently) seen as a case of a more open mutualism. Plants profit from the dispersal service that some frugivores give them, while such frugivores profit from the fruits as food. However, in this mutualism single frugivore actors can be more easily replaced by other species of the same ecological guild than in coevolving matching pairs (of organisms). The plant-frugivore mutualism also allows certain asymmetries in the relationships, e.g. a disperser does not need to be specialized in only one size or type of fruits, and a plant does not necessarily have to depend on only one disperser. Under such circumstances, the question is to what extent fruit users are able to exert selection on fruit traits. The topic has been put on hold, as the focus of research has shifted towards the dispersion patterns created by animal seed dispersers and the consequences for recruitment (see Nathan and Muller-Landau 2000). Still, the question of possible selection pressures by frugivores remains open. Neotropical strangler figs are an example of a situation where fruit traits may be shaped by a guild of consumers, rather than by single frugivore species. Bird-dispersed species have red figs (when ripe) that ripen asynchronously over relatively long periods and produce little scent, while bat-dispersed species have “green(ish)” figs that are larger, span a range of sizes, ripen relatively synchronously, and produce very distinctive aromas (Kalko et al. 1996; Korine et al. 2000). This is, however, a special case of canopy plants with very prominent and large fruit display and many species of frugivores. Field studies are needed for more and different plant growth types and different numbers of fruit users.

A testable framework of the plant-frugivore interactions in tropical forests has been provided by Howe and coworkers with the “specialist” versus the “generalist” dispersal system (Howe and Estabrook 1977; Howe and Smallwood 1982; Howe 1993). These authors contrasted “trees that produce scarce but especially nutritious fruits that entrain specialized and reliable dispersal agents and other tree species that produce common but less nutritious fruits and appeal to individually less reliable but collectively more common species of opportunistic dispersal agents”.

In the Amazonian rain forest of eastern Ecuador, I conducted a field study on the dispersal ecology of *Leonia cymosa* (Violaceae), an understorey tree that grew to a mean height of 7 m and a maximum height of 13 m in my study plots. Indigenous people of the study area reported that tamarins feed on this tree. *L. cymosa*’s size made it possible to quantify fruit production and fruit removal by means of full counts. Furthermore, I conducted observations, nutritional analysis of fruits, and measurements of growth parameters and neighborhood conditions of trees. I analyzed the data obtained using multivariate statistical tools.

Leonia cymosa clearly groups into the specialist dispersal system, from the tree’s side as well as from the frugivores’ side. *L. cymosa* produced small median and maximum seasonal fruit crop sizes of large fruits with large seeds. Its fruit pulp offered not only sugar, but also a median content of proteins of almost 20% dry weight (chapter 3.1). Fruit ripening was prolonged, which has been pointed out as strategy to avoid saturation of dispersers in bird-dispersed trees (Howe and Estabrook 1977). This way of fruit display might indeed favor a better usage of the only reliable seed disperser of *L. cymosa* I observed, the Black mantle tamarin (*Saguinus nigricollis*). Tamarin groups visited study plots every two days (mean interval: 1.8 days), exploiting several yet not all trees. They had a limited capacity of removing fruits from single trees, due to their small group sizes and their way of treating the fruits of *L. cymosa*. Tamarins opened up the outer woody fruit peel and took out seeds surrounded by fruit pulp, which they swallow all together (chapter 3.2). This behavior resulted in a series of far distance dispersal events.

S. nigricollis is not purely, but consistently frugivorous. It depends to a large extent on a fruit diet (compiled from Ulloa 1988; Emmons 1990; de la Torre 1991; Garber 1993; Peres 1993; de la Torre et al. 1995; Lima and Ferrari 2003). Its habit of seed swallowing is consistent with similar behavior of other species of the genus, e.g. *S. fuscollis*, and *S. mystax*. Of these species it is also known that they deposit seeds either singly or in clumps of only a small number of seeds (Knogge 1999; Knogge and Heymann 2003). Such seed treatment makes tamarins almost “ideal” seed dispersers, because it reduces sibling competition of seedlings and saplings (Schupp 1993) and may even reduce attacks of seed predators compared with a seed deposition in larger clumps (Howe 1989). *S. fuscicollis* and *S. mystax* have a remarkable capacity to swallow very large seeds in relation to their body size. Yet they do not disperse the seeds of all fruits they eat. Where possible, they separate seeds from fruit pulp. Seeds are swallowed only when the fruit pulp is firmly attached to the seeds (Knogge and Heymann 2003). This is exactly the case in *L. cymosa*, which has an extremely sticky fruit pulp that is inseparable from the single seed. It is the key to the close interaction of the tamarins with *L. cymosa*, paired with *S. nigricollis*’s ability to swallow large seeds, or even its suggested need to swallow large seeds to maintain gastrointestinal health (Heymann 1992; Garber and Kitron 1997).

L. cymosa is thus an example of a plant that can, in some cases, avoid giving the reward before having secured the dispersal service. Fruit pulp firmly attached to the seed has not yet been recognized as a way that plants can manipulate potentially seed-dispersing frugivores. Other means known so far of plants to influence fruit removal and seed dispersal are substances in the fruit pulp of unripe fruits acting as feeding deterrents (Cipollini and Levey 1997; Schaefer et al. 2003), ensuring that fruits are removed only when they are fully developed and bear viable seeds. Furthermore, hard fruit peels and large seed size may generally exclude a wide range of fruit users. However, the adaptive value of e.g. large sized seeds may be a compensation of loss of seed mass to invertebrate attack during germination and seedling establishment (Hammond and Brown 1998), rather than allowing only few frugivores to use the fruits.

Although some studies indicate that the species numbers and the abundance of frugivores is lower in the under storey of rain forests than in the canopy (e. g. Murray 1987; Bernard 2001; Kalko and Handley 2001; Henry et al. 2004), it was surprising to find a very small number of species feeding on fruits of *L. cymosa*. In addition to tamarins, only squirrel monkeys (*Saimiri sciureus*) were found to exploit *L. cymosa*. Squirrel monkeys visited my study plots less frequently, yet removed large numbers of fruits. They handled *L. cymosa*'s seeds in a completely different way than tamarins. They did not swallow the seeds, despite the sticky fruit pulp, but spat them out after having sucked and gnawed the pulp (chapter 3.2), which is consistent with the observation of other researchers that squirrel monkeys generally ingest only very small seeds (S. Boinski, personal communication). Thus, this fruit user dropped the seeds of *L. cymosa* under the crown of the trees they visited. The seeds stayed intact, yet most of them were consumed by rodents. Only occasionally may squirrel monkeys have taken entire fruits away to neighboring trees. Therefore, compared to the fruit removal by tamarins, fruit removal by squirrel monkeys did not contribute to seed dispersal, but generally involved the loss of seeds.

My findings show that tamarins play a crucial role in the dispersal system of *L. cymosa*. Fruits of *L. cymosa* and of *L. glycicarpa* rank high in the diet of tamarins throughout the Amazonian rain forest (Terborgh 1983; Knogge 1999). They are, for example, a preferred food relative to occurrence in *S. fuscicollis* (Peres 1993). I conclude that a close interaction exists between *L. cymosa* and *S. nigricollis,* opening the possibility to observe selection by the frugivore on traits of the tree in this dispersal system.

The question whether dispersers exert selection pressures has several aspects. 1) Do they choose according to the fruits' nutrient content? 2) Does this lead to differential fruit removal from tree individuals and do preferred tree individuals gain a higher dispersal that way? 3) How do dispersers react to other tree characters and the conditions in the neighborhood of a tree? And finally, 4) how do other frugivores react to the same factors? Do non-dispersing frugivores counteract selection of dispersers?

The relation between fruit removal and macronutrients in the fruit pulp has been studied in various taxa (e.g.Bonaccorso and Gush 1987; Barton and Whiten 1994; Fietz and Ganzhorn 1999; Riba-Hernandez et al. 2003; Schaefer et al. 2003; Norconk and Conklin-

Brittain 2004), showing that frugivores often choose fruits in accordance with optimal diet theory (Stephens and Krebs 1986). Yet most of the studies so far have considered only choices between different fruit species. Fruit selection within a plant species has only rarely been the focus of study (Foster 1990; Schaefer and Schmidt 2002), and frugivores' fruit choice has so far not been linked with individual dispersal success. Tamarins, the reliable seed dispersers of *L. cymosa*, have a highly sensitive sense of taste for the sugars present in the fruit pulp of *L. cymosa*. Several species of the genus *Saguinus* are especially stimulated by fructose and sucrose (Glaser 1986; Simmen 1992; Simmen and Hladik 1998). Individual trees of *L. cymosa* showed a clearly distinguishable composition of the nutrient content of their fruits (chapter 3.1). Thus, this dispersal system appeared very suitable to test the influence of the nutritional quality on dispersal success. I did this with a set of large trees with comparable, large seasonal production of ripe fruits, defining dispersal success as the total of fruits removed by tamarins throughout the fruiting season. Surprisingly, fruit removal by tamarins was not attributable to contents of single nutrients or energy content of the fruits (chapter 4.1.). I could thus not confirm my hypothesis of a differential dispersal success of individual trees mediated through fruit nutrient content – as far as reflected by the nutritional components measured – and consequently no selection of the disperser on nutritional quality, at least not a fine-tuned one. Dispersers could still exert selection on fruit quality by exploiting only fruits with a minimum requirement of nutrients. All trees included in my analysis did seem to meet this requirement. Though not differentiating between single sources of fruits of *L. cymosa*, tamarins could still forage in accordance with optimal diet theory because *L. cymosa* might be rich in sugar and proteins relative to other fruit resources available at the same time.

The effect of nutrients on food choice could also have been overlaid by growth traits and differences in the regime of fruit display of the trees, by predation risk in a tree, or by the con-specific fruit supply in the neighborhood of the *L. cymosa*- trees. The latter has been demonstrated in studies of bird-dispersed plants. For example, Sargent (1990) found enhanced fruit removal rates, whereas Denslow (1987) found inhibited fruit removal rates at high neighborhood fruit density. Likewise, Manasse (1983) observed reduced fruit removal by several bird species and one monkey species in clusters of *Virola* trees as compared to stand-alone trees, and concluded that trees in tropical rain forests compete for seed dispersers. I studied such potential determinants of fruit removal in a separate approach using a larger tree sample size that enabled a multivariate analysis.

Tamarins were less likely to harvest *Leonia* trees that were not or less completely covered by surrounding vegetation, which probably reflects a behavior to avoid predation by forest raptors. The con-specific fruit supply in the neighborhood of a *Leonia* tree neither enhanced nor reduced the number of its fruits removed throughout the fruiting season. However, at high con-specific fruit abundance in the neighborhood, the proportion of fruits removed by tamarins was reduced (chapter 4.2). This suggests competition among trees for the seed-dispersing monkey. Thus, neighborhood conditions indeed influenced fruit removal in *L. cymosa* and may constrain the selective pressure of frugivores on traits of the tree.

Concerning the regime of fruit display of the trees, I considered in my models (a) the synchrony of fruit ripening of an individual tree with the rest of the population in the plots, and (b) the individual distribution of ripe fruits produced over the entire fruiting season (ranging from comparatively peaked to comparatively constant). Neither of the two characters describing the individual fruiting pattern was related to fruit removal by *S. nigricollis* (chapter 4.2). Given small fruit removal capacity of tamarins at a single visit, fruiting was long enough in all trees under all fruiting patterns to enable repeated visits of tamarins, and all trees seemed to fruit for a time span long enough to avoid rapid saturation of dispersers (cf. Howe and Estabrook 1977 for bird-dispersed trees).

As part of their theoretical models on tropical dispersal systems, Howe and Estabrook (1977) put forward a hypothesis on the selective influence of frugivores on fruit crop sizes of plants, which was later termed fruit crop size hypothesis (below: FCSH). It states that both a larger dispersal success (no. of fruits removed by the effectively seed-dispersing frugivores) and a higher dispersal efficiency (% of fruits removed by the effectively seed-dispersing frugivores) in large fruit crops would select for crops growing to large sizes, a process being limited by the density of dispersal agents. Some studies of bird dispersal confirmed the predictions of the FCSH (Sargent 1990; Ortiz-Pulido and Rico-Gray 2000), while others gave only partial support (relation between no. of fruits removed and crop size: Davidar and Morton 1986; Denslow 1987; Murray 1987; Willson 1988; Carr 1992; French et al. 1992; Willson and Whelan 1993), or no support (Thébaud and Debussche 1992; Laska and Stiles 1994; Traveset 1994). Only Russo (2003) studied the relation of fruit crop size with fruit removal by seed-dispersing monkeys. In this study, spider monkeys removed more seeds of *Virola calophylla* (Myristicaceae) the more ripe fruits were available in the tree crown at the moment of their visit. Except for Russo (2003), and (Murray 1987), none of the authors cited above treated the effect of fruit crop size on visitation of fruiting plants, though it can be derived from FCSH that fruit crop size should also have an effect on the initial step of fruit removal, which is the detection of a fruit resource and the decision of frugivores to feed on it.

In my study system, comprising *L. cymosa* and its fruit consumers, fruit crop size was by far the most important predictor of all aspects of fruit removal, by the effective disperser, *Saguinus nigricollis*, as well as by the non-disperser, *Saimiri sciureus* (chapter 4.2). Trees with larger seasonal fruit crop size had a higher probability to have fruits removed by the disperser than those with small seasonal fruit crop sizes. They also had a higher number of fruits removed by the seed disperser, i.e. a higher dispersal success. However, the proportion of fruits removed by the disperser, i.e. the dispersal efficiency of an individual tree, decreased with increasing seasonal fruit crop size, indicating a saturation of the tamarins. In contrast, the probability of fruit removal by the non-disperser, as well as the number of fruits and the proportion of fruits removed by it increased with seasonal fruit crop sizes. The observed differences between disperser and non-disperser are due to differences in feeding capacity, group size and foraging behavior (chapter 3.2 and 4.2).

These findings reveal a selection of the disperser on the seasonal fruit crop size of *L. cymosa* and corroborate the fruit crop size hypothesis (FCSH) for a monkey-dispersed tree species. Consistent with the FCSH, large seasonal fruit crop sizes were favored by the increasing number of fruits removed by the disperser, which is a direct correlate of fitness because of pervasive negatively density-dependent recruitment in tropical forests (Harms et al. 2000). Furthermore, the disperser preferred to visit (and harvest) large fruit crops. The importance of large fruit crop sizes for the chance of visitation by the seed disperser may, however, be case-specific, because e.g. in *Virola calophylla* visitation by spider monkeys did not depend on the (standing) crop size (Russo 2003, yet visitation of spider monkeys and several species of seed dispersing birds together depended on the number of fruits available). In *L. cymosa*, fruit removal capacity and availability of the disperser are low, and consequently, dispersal efficiency of individual trees can only grow to a small extent with fruit crop size. In accordance with FCSH, this may limit fruit crop sizes, because energy allocated to too many fruits undispersed seeds may be wasted.

Trees of *L. cymosa* also lose a large portion of their fruit production to fruit removal by squirrel monkeys. My data suggest that *L. cymosa*'s fruit crop sizes may be stabilized not only by disperser density, but also by fruit removal of non-dispersing frugivores. Thus, fruit removal by the non-dispersing frugivore would not counteract selection of seed dispersers on the fruiting tree, but supports it. FCSH appears a valid framework also in the monkey-dispersed *Leonia*. However, my results show that the probability of visitation by dispersers and the role of non-dispersers should be included in this framework.

References

Barton, R. A. and A. Whiten (1994). Reducing complex diets to simple rules - food selection by olive baboons. Behavioral Ecology and Sociobiology 35: 283-293.

Bernard, E. (2001). Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. Journal of Tropical Ecology 17: 115-126.

Bonaccorso, F. J. and T. J. Gush (1987). Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: an experimental study. Journal of Animal Ecology 56: 907-920.

Carr, D. E. (1992). The relationship between crop size and fruit removal and its implication for the evolution of dioecy. Canadian Journal of Botany 70: 1784-1789.

Chapman, C. A. and D. A. Onderdonk (1998). Forests Without Primates: Primate/Plant Codependency. American Journal of Primatology 45: 127-141.

Cipollini, M. L. and D. J. Levey (1997). Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. American Naturalist 150: 346–372.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of Populations, Proceedings of the Advanced Study Institute on 'Dynamics of Numbers in Populations', Oosterbeek, NL, 7-18 September 1970. P. J. den Boer and G. R. Gradwell. Wageningen, Centre for Agricultural Publishing and Documentation: 298-312.

Davidar, P. and E. S. Morton (1986). The relationship between fruit crop sizes and fruit removal rates by birds. Ecology 67: 262-265.

de la Torre, S. (1991) Area de vida, comportamiento reproductivo y habitat de *Saguinus nigricollis graellsi* (Primates: Callitrichidae) en la Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 162

de la Torre, S., F. Campos and T. de Vries (1995). Home range and birth seasonality of Saguinus nigricollis graellsi in Ecuadorian Amazonia. American Journal of Primatology 37: 39-56.

Denslow, J. S. (1987). Fruit removal rates from aggregated and isolated bushes of the red elderberry, Sambucus pubens. Canadian Journal of Botany 65: 1299-1235.

Emmons, L. H. (1990). Neotropical Rainforest Mammals: A Field Guide. Chicago and London, The University of Chicago Press.

Fietz, J. and J. U. Ganzhorn (1999). Feeding ecology of the hibernating primate Cheirogaleus medius : how does it get so fat? Oecologia 121: 157-164.

Foster, M. S. (1990). Factors influencing bird foraging preferences among conspecific fruit-trees. Condor 92: 844-854.

French, K., D. J. O'Dowd and A. Lill (1992). Fruit removal of Coprosma quadrifida (Rubiaceae) by birds in south-eastern Australia. Australian Journal of Ecology 17: 35-42.

Garber, P. A. (1993). Feeding ecology and behavior of the genus Saguinus. Marmosets and Tamarins. Systematics, Behavior, and Ecology. A. B. Rylands. New York, Oxford University Press: 273-295.

Garber, P. A. and U. Kitron (1997). Seed swallowing in tamarins: evidence of a curative function or enhanced foraging efficiency? International Journal of Primatology 18: 523-538.

Glaser, D. (1986). Geschmacksforschung bei Primaten. Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 131: 92-110.

Hammond, D. S. and V. K. Brown (1998). Disturbance, phenology and life-history characteristics: Factors influencing distance/density-dependent attack on tropical seeds and seedlings. Dynamics of tropical Communities. The 37th symposium of the British Ecological Society Cambridge University. D. M. Newbery, H. H. T. Prins and N. D. Brown, Blackwell Science: 51-78.

Harms, K. E., S. J. Wright, O. Calderón, A. Hernández and E. A. Herre (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404: 493-495.

Henry, M., P. Barriere, A. Gautier-Hion and M. Colyn (2004). Species composition, abundance and vertical stratification of a bat community (Megachiroptera : Pteropodidae) in a West African rain forest. Journal of Tropical Ecology 20: 21-29.

Herrera, C. M. (1985). Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44: 132-141.

Heymann, E. W. (1992). Seed ingestion and gastrointestinal health in tamarins? Laboratory Primate Newsletters 31: 15-16.

Howe, H. F. (1989). Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79: 417-426.

Howe, H. F. (1993). Specialized and generalized dispersal systems: where does 'the paradigm' stand? Vegetatio 107/108: 3-13.

Howe, H. F. and G. F. Estabrook (1977). On intraspecific competition for avian dispersers in tropical trees. American Naturalist 111: 817-832.

Howe, H. F. and J. Smallwood (1982). Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13: 201-228.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501-521.

Jordano, P. (2000). Fruits and frugivory. Seeds - the ecology of regeneration of plant communities. M. Fenner, Chapman and Hall.

Kalko, E. K. V. and C. O. Handley (2001). Neotropical bats in the canopy: diversity, community structure, and implications for conservation. Plant Ecology 153: 319-333.

Kalko, E. K. V., E. A. Herre and C. O. Handley (1996). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. Journal of Biogeography 23: 565-576.

Knogge, C. (1999). Tier-Pflanze-Interaktion im Amazonas-Regenwald: Samenausbreitung durch die sympatrischen Tamarinarten Saguinus mystax und Saguinus fuscicollis (Callitrichidae, Primates). Münster, Schüling Verlag.

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.

Knott, C. D. (1998). Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. International Journal of Primatology 19: 1061-1079.

Korine, C., E. K. V. Kalko and E. A. Herre (2000). Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. Oecologia 123: 560-568.

Laska, M. S. and E. W. Stiles (1994). Effects of fruit crop size on intensity of fruit removal in Viburnum prunifolium (Caprifoliaceae). Oikos 69: 199-202.

Lima, E.-M. and S.-F. Ferrari (2003). Diet of a free-ranging group of squirrel monkeys (Saimiri sciureus) in eastern Brazilian Amazonia. Folia Primatologica 74: 150-158.

Manasse, R. M. and H. F. Howe (1983). Competition for dispersal agents among tropical trees: influences of neighbors. Oecologia 59: 185-190.

McKey, D. (1975). The ecology of coevolved seed dispersal systems. Coevolution of animals and plants. L. E. Gilbert and P. H. Raven. Austin, Texas, University of Texas Press: 159-191.

Murray, K. G. (1987). Selection for optimal fruit-crop size in bird-dispersed plants. The American Naturalist 129: 18-31.

Nathan, R. and H. C. Muller-Landau (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278-285.

Norconk, M. A. and N. L. Conklin-Brittain (2004). Variation on frugivory: The diet of Venezuelan white-faced sakis. International Journal of Primatology 25: 1-26.

Ortiz-Pulido, R. and V. Rico-Gray (2000). The effect of spatio-temporal variation in understanding the fruit crop size hypothesis. Oikos 91: 523-527.

Peres, C. A. (1993). Diet and feeding ecology of saddle-back (Saguinus fuscicollis) and moustached (S. mystax) tamarins in an Amazonian terra firme forest. J. Zool., Lond. 230: 567-592.

Riba-Hernandez, P., K. E. Stoner and P. W. Lucas (2003). The sugar composition of fruits in the diet of spider monkeys (Ateles geoffroyi) in a tropical humid forest in Costa Rica. Journal of Tropical Ecology 19: 709-716.

Russo, S. E. (2003). Responses of dispersal agents to tree and fruit traits in Virola calophylla (Myristicaceae): implications for selection. Oecologia 136: 80-87.

Sargent, S. (1990). Neighborhood effects on fruit removal by birds: a field experiment with Viburnum dentatum (Caprifoliaceae). Ecology 71: 1289-1298.

Schaefer, H. M. and V. Schmidt (2002). Vertical stratification and caloric content of the standing fruit crop in a tropical lowland forest. Biotropica 34: 244-253.

Schaefer, H. M., V. Schmidt and H. Winkler (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. Oikos 102: 318-328.

Schupp, E. W. (1993). Quantity, Quality and the Effectiveness of Seed Dispersal by Animals. Vegetatio 108: 15-29.

Simmen, B. (1992). Taste thresholds and above-threshold responses to fructose in callitrichid primates with reference to diet. Comptes Rendus de l'Academie de Sciences Série III Sciences de la Vie 315: 151-57.

Simmen, B. and C. M. Hladik (1998). Sweet and bitter taste discrimination in primates: scaling effects across species. Folia Primatologica 69: 129-138.

Snow, D. W. (1971). Evolutionary aspects of fruit-eating birds. Ibis 113: 194-202.

Stephens, D. W. and J. R. Krebs (1986). Foraging Theory. Princeton, New Jersey, Princeton University Press.

Terborgh, J. (1983). The use of plant resources (chapter 5), Foraging for prey (chapter 6). Five new world primates: a study in comparative ecology. J. Terborgh. Princeton, N.J., Princeton Univ. Pr.

Thébaud, C. and M. Debussche (1992). A field test of the effects of infructescens size on fruit removal by bird in Vibirnum tinus. Oikos 65: 391-394.

Traveset, A. (1994). Influence of type of avian frugivory on the fitness of Pistacia terebinthus L. Evolutionary Ecology 8: 618-627.

Ulloa, R. (1988) Estudio sinecologico de primates en la Reserva de Producción Faunistica Cuyabeno, Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 179

van der Pijl, L. (1969). Principles of dispersal in higher plants. Berlin, Springer.

Webb, C. O. and D. R. Peart (2001). High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. Ecology Letters 4: 491-499.

Wheelwright, N. and G. Orians (1982). Seed dispersal by animals - contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist 119: 402-413.

Willson, M. F. (1988). Phenology of vertebrate removal of Myoporum acuminatum fruits in a Queensland forest. Evolutionary Ecology 2: 282-288.

Willson, M. F. and C. J. Whelan (1993). Variation of dispersal phenology in a bird-dispersed shrub, Cornus drummondii. Ecological Monographs 63: 151-172.

6 Summary

Leonia cymosa (Violaceae) is a small tree from the under story of the Amazonian rain forest. As far as currently documented by botanical collections, it is distributed in the rain forests of western Amazonia near the Andes and the Guyana shield. No details were known on the ecology and life history of *L. cymosa* before this study. I investigated the seed dispersal ecology of *L. cymosa* in plots of old growth terra firme forest located within the Cuyabeno Faunistic Reserve in north-eastern Ecuador. Local indigenous people knew that monkeys disperse the seeds of *L. cymosa*. Because of its size, relatively high abundance, and the countable number of fruits it produces, this species offered good conditions to examine the variation of traits of individual trees and the way they are linked with fruit removal from each tree. With this study I aimed to address the question whether frugivores exert selection pressures on fruits and the fruiting regime of fleshy fruited plants. Furthermore, by choosing *L. cymosa* I aimed to assess the applicability of the hypotheses on frugivory, developed mainly for bird-dispersed plants, to monkey-dispersed plant species.

From 1998 to 2001 I monitored the flowering and fruiting activity of a population of trees in the forest near the Laguna Grande de Cuyabeno (0°2'N 76°15'W, elevation 250 m). I took tree measurements and mapped the spatial distribution of fruiting trees. In two fruiting seasons, one in 1999 and one in 2000, I determined the fruit production of a sample of individual trees. I analyzed the nutritional content of the fruit pulp of fruits from a sub-sample of trees in the fruiting season of 2000. By means of direct observation, and assisted by automatic cameras, I examined the assemblage of fruit users of *L. cymosa*, as well as their respective qualities as seed dispersers. Parallel to the monitoring of fruit production I determined fruit removal from the same trees, applying repeated full counts of fruits in the tree crowns. I related fruit removal to variables describing tree traits and neighborhood conditions, using univariate and multivariate statistics.

The main findings of this study are:

- The mean height of a fruiting *L. cymosa* was 6.6 m (range: 2 - 12.6 m). The median tree density was 11.8 trees per hectare. Trees grew in clusters consisting of different numbers of trees of different heights.

- *L. cymosa* flowered two times a year, in late February to March and in October. The respective fruiting seasons occurred in August/September and between March and May. The reproductive pattern is in accordance with the hypothesis that changes in sunset times at the equinoxes trigger flower development at the Equator.
- The fruit pulp of *L. cymosa* contained the sugars fructose, glucose, and sucrose, the total soluble sugar being the first important nutritional compound of the fruit pulp. The second important compound was proteins. No lipids were found in the fruit pulp, and amino acids occurred only in traces with concentrations close to the detection limit.
- The variation of nutritional quality of the fruits was high within trees. Nonetheless, significant differences were found among trees in all nutrient constituents studied.
- The maximum of ripe fruits produced per season by a single tree was 427. Median productivity of the trees was 45 ripe fruits throughout the fruiting season in 1999 and 36 ripe fruits in 2000. Seasonal fruit production was weakly correlated with tree size in 1999, yet not significantly correlated with tree size in 2000. The maximum standing crop of fruits in a tree was 324 fruits (counted in 2000). However, 75% of the trees had standing crops of only up to 20 ripe fruits in 1999 and up to 30 ripe fruits in 2000.
- Black mantle tamarins, *Saguinus nigricollis* (Callitrichidae), and squirrel monkeys, *Saimiri sciureus* (Cebidae), and possibly an unknown nocturnal frugivore consumed the fruits of *L. cymosa* at my study site. Green-rumped acouchis (*Myoprocta pratti*, Dasyproctidae) consumed fallen fruits and seeds underneath the trees.
- Black mantle tamarins and squirrel monkeys differed widely in their effectiveness as seed dispersers. Black mantle tamarins swallowed the seeds together with the fruit pulp and defecated intact seeds far away from the mother tree. Squirrel monkeys opened the fruits to suck and gnaw on the fruit pulp, and then dropped seeds to the forest floor below the tree crowns. Squirrel monkeys might have occasionally carried fruits to neighboring trees. Thus, fruit removal by tamarins almost completely accounted for seed dispersal. Squirrel monkeys, on the other hand, did not disperse seeds, or at best in minimal numbers.
- 55% of all feeding visits recorded in the fruiting season of 2000 were visits by tamarins, whereas 45% were visits by squirrel monkeys. Yet squirrel monkeys in total harvested almost three times more fruits of *L. cymosa* than tamarins due to their larger group size (ca. 30 individuals versus 6-9 individuals of tamarins per group) and other

feeding technique. Tamarins visited the study plots more frequently than squirrel monkeys (in one plot e.g. mean interval between harvest of 1.8 days versus 4.3 days), and tamarins fed on fewer trees per visit in a plot than squirrel monkeys (in one plot e.g. mean number of trees exploited per visit of 3.2 versus 7.8). In a single tree, tamarins harvested from 1 to 25 fruits per visit, while squirrel monkeys harvested from 1 to 224 fruits per visit. Both monkey species left ripe fruits behind in the tree crowns in 97% of all feeding events. Both monkey species together consumed 9% of the ripe fruits produced by all trees monitored during the fruiting season of 1999, and roughly 50% of the ripe fruits produced by all trees monitored in the fruiting season of 2000. The conspicuous difference between the two years was in part due to the fact that in 1999 30% of the overall number of fruits were infested with lepidopteran larvae and were discarded by the trees prior to removal by frugivores, whereas no such infestation could be found in 2000.

- Each of my study plots fell into the core home range of one group each of *S. nigricollis* and *S. sciureus*. Thus, the frugivore assemblage is small and disperser availability is limited for the individual tree of *L. cymosa*.
- The criteria of a “specialist dispersal system” as summarized by Howe et al. (1977) apply to the traits of *L. cymosa*, as well as to the frugivore side of its dispersal system. Black mantle tamarins are obviously important seed dispersers for *L. cymosa*. The interaction between *S. nigricollis* and *L. cymosa* seems close enough to expect a potential for selective influences of the seed disperser on fruit or fruiting traits of the tree.
- In a sample of 6 trees of comparable and high fruit crop size, the total of ripe fruits removed from a tree throughout the whole fruiting season by the reliable seed disperser *S. nigricollis* was neither significantly correlated with the content of any of the nutrients measured in the fruit pulp (fructose, glucose, sucrose, total protein; pulp does not contain lipids), nor with total metabolisable energy, seed to pulp weight ratio, or water content of the fruit pulp. Feeding preferences for single sugars determined by other laboratory studies were not confirmed by this field study. The reliable seed disperser *S. nigricollis* does not seem to exert selective pressure on the nutrient content of the fruits of *L. cymosa*.
- Seasonal fruit crop size was the main predictor of all aspects of fruit removal by the effective disperser of *L. cymosa*, *Saguinus nigricollis*, as well as by the non-disperser,

Saimiri sciureus. Trees with larger seasonal fruit crop size had a higher probability to have fruits removed by the disperser than those with small seasonal fruit crop sizes. They also had a higher number of fruits removed by the seed disperser, i.e. a higher dispersal success. However, the proportion of fruits removed by the disperser, i.e. the dispersal efficiency of an individual tree, decreased with increasing seasonal fruit crop size. In contrast, probability of fruit removal, the number of fruits removed, and the proportion of fruits removed by the non-disperser increased with increasing seasonal fruit crop sizes. The observed differences between disperser and non-disperser are due to differences in feeding capacity, group size and foraging behavior.

- Tamarins were less likely to harvest *Leonia* trees that were not or less completely covered by surrounding vegetation. This probably reflects a behavior to avoid predation by forest raptors.
- At high con-specific fruit abundance in the neighborhood, the proportion of fruits removed by tamarins was reduced. This suggests competition of trees for the disperser.
- My study revealed selection of the disperser on seasonal fruit crop size of *L. cymosa*. Consistent with the “fruit crop size hypothesis” (FCSH), large seasonal fruit crop sizes were favored by the increasing number of fruits removed by the disperser, as well as by being preferably visited (and harvested) by the disperser. On the other hand, the decreasing dispersal efficiency of large fruit crop sizes seems to cause selection against outstandingly high fruit crop sizes (stabilizing selection).
- My data suggest that fruit removal by the non-disperser selects against large fruit crop size via fruit waste in the same way.
- FCSH appears to constitute a valid framework also in the monkey-dispersed *L. cymosa*. However, my results show that the probability of visitation by dispersers and the role of non-dispersers should be included in this framework. My findings also show that factors beyond the tree’s control influenced fruit removal from *Leonia* trees. Disperser-mediated selection may be constrained (yet not impeded) by neighborhood conditions.

Zusammenfassung

Leonia cymosa (Violaceae) ist ein Baum der unteren Waldschicht im Amazonischen Regenwald. Soweit bisher durch botanische Sammlungen dokumentiert, umfasst das Verbreitungsgebiet von *L. cymosa* West-Amazonien nahe den Anden und den Guyanaschild. Vor dieser Studie waren keine Details über die Ökologie und Lebensgeschichte von *L. cymosa* bekannt. Ich habe die Samenausbreitungsökologie von *L. cymosa* in einem alten Bestand von „terra-firme"-Regenwald untersucht. Meine Probenflächen befanden sich in der „Reserva Faunistica Cuyabeno" im nord-östlichen Ecuador. Den lokalen indigenen Bewohnern der Rerserva war bekannt, dass Affen die Samen von *L. cymosa* ausbreiten. Meine Untersuchung hatte das Ziel, die Variation von Baummerkmalen zu beschreiben und zu klären, ob und wie die Fruchtentnahme aus den einzelnen Bäumen durch Fruchtfresser mit den Baummerkmalen zusammenhängt. Aus den Ergebnissen dieser Untersuchung lassen sich Rückschlüsse ziehen, ob Fruchtfresser Selektionsdruck auf Fruchtmerkmale oder das Muster der Fruchtreifung ausüben. Wegen seiner relativ geringen Größe, seiner Häufigkeit und der zählbaren Anzahl an Früchten, die der einzelne Baum produziert, bot der Baum *L. cymosa* sehr gute Bedingungen für eine solche Untersuchung. Meine Wahl fiel auch deswegen auf *L. cymosa* als Untersuchungsobjekt, weil ich prüfen wollte, ob sich Hypothesen zur Interaktion von Pflanzen und Fruchtfressern, die am Beispiel von vogelverbreiteten Pflanzen entwickelt wurden, auch bei Verbreitung durch Affen anwenden lassen.

Von 1998 bis 2001 wurden das Blüh- und die Fruchtreifungsgeschehen einer Baumpopulation in der Nähe der Laguna Grande de Cuyabeno (0°2'N 76°15'W, 250 m über NN) überwacht. In zwei Fruchtsaisons, eine 1999 und eine im Jahr 2000, wurde die Fruchtproduktion einer Stichprobe von Bäumen bestimmt. Die Bäume wurden außerdem vermessen und ihr Standort wurde kartiert. Mit Beobachtungen, unterstützt durch automatische Kameras, wurden die Fruchtnutzer von *L. cymosa* erfasst, sowie ihre jeweilige Qualität als Samenausbreiter bestimmt. Parallel zur Überwachung der Fruchtproduktion wurde in denselben Bäumen die Fruchtentnahme quantifiziert, beides durch Zählungen aller jeweils vorhandenen Früchte in den Baumkronen. Die Fruchtentnahme wurde mit Variablen in Bezug gesetzt, die einzelne Bäume und die

Bedingungen in ihrer Nachbarschaft beschrieben. Der mögliche Einfluss dieser Variablen auf die Fruchtentnahme wurde mit univariaten und multivariaten Statistiken untersucht.

Die wesentlichen Ergebnisse meiner Arbeit sind:

- Die mittlere Höhe einer fruchttragenden *L. cymosa* war 6,6 m (Min. 2 m, Max. 12,6 m). Der Median der Individuendichte lag bei 11,8 Bäumen pro Hektar. Die Bäume wuchsen überwiegend in Gruppen, die aus Bäumen verschiedener Höhe bestanden.
- *L. cymosa* blühte zwei Mal im Jahr, sowohl im späten Februar bis März, als auch im Oktober. Die daraus jeweils folgenden Fruchtsaisons erstreckten sich auf die Monate August/September und März bis Mai. Dieses Muster der Reproduktionsaktivität stimmt mit der Hypothese überein, dass am Äquator Verschiebungen der Sonnenuntergangszeiten zu den Tagundnachtgleichen die Blütenbildung auslösen.
- Das Fruchtfleisch von *L. cymosa* enthielt die Zucker Fruktose, Glucose und Saccharose. Die gesamten löslichen Zucker waren die wichtigste Nährstoffkomponente des Fruchtfleischs. Die zweitwichtigste Nährstoffkomponente waren Proteine. Lipide waren im Fruchtfleisch nicht enthalten. Aminosäuren kamen in Spuren am Rande der Nachweisgrenze vor.
- Innerhalb der Bäume war die Variation des Nährstoffgehalts der Früchte groß. Dennoch gab es signifikante Unterschiede zwischen Bäumen bei allen untersuchten Nährstoffbestandteilen.
- Die saisonale Produktivität der überwachten Bäume lag in der Fruchtsaison von 1999 im Median bei 45 reifen Früchten (Maximum: 363 reife Früchte, Minium: 12 Reife Früchte und in der Fruchtsaison von 2000 im Median bei 36 reifen Früchten (Maxium: 427 reife Früchte, Minium: 1 reife Früchte). Die saisonale Fruchtproduktion war im Jahr 1999 schwach korreliert mit der Baumgröße. Im Jahr 2000 bestand keine signifikante Korrelation zwischen Fruchtproduktion und Baumgröße. Das maximale Fruchtangebot eines Baumes zum Zeitpunkt einer Fruchtzählung lag bei 324 reifen Früchten (gezählt in der Saison 2000). 75% aller Bäume hatten jedoch Fruchtangebote von bis zu 20 reifen Früchten während der Fruchtsaison 1999 und von bis zu 30 reifen Früchten während der Fruchtsaison 2000.
- Schwarzrückentamarine (*Saguinus nigricollis*, Callitrichidae) und Totenkopfäffchen (*Saimiri sciureus*, Cebidae), sowie möglicherweise eine unidentifizierte nachtaktive

Tierart, konsumierten die Früchte von *L. cymosa* in meinem Untersuchungsgebiet. Früchte, die von den Bäumen auf den Boden herabgefallen waren, wurden von Grünen Zwergagutis (*Myoprocta pratti*, Dasyproctidae) gefressen.

- Schwarzrückentamarine und Totenkopfäffchen unterschieden sich stark in ihrer Effektivität als Samenausbreiter. Schwarzrückentamarine verschluckten die Samen zusammen mit dem Fruchtfleisch und schieden intakte Samen in großer Entfernung von den Mutterbäumen wieder aus. Totenkopfäffchen saugten und nagten am Fruchtfleisch um die Samen, ließen dann aber die so behandelten Samen auf den Waldboden unter den Baum fallen. In wenigen Fällen könnten Totenkopfäffchen ganze Früchte in benachbarte Bäume mitgenommen haben. Während also die Fruchtentnahme durch Tamarine fast vollständig zur Samenausbreitung beitrug, breiteten die Totenkopfäffchen keine Samen aus, oder nur in sehr geringer Zahl.
- Von allen Fressbesuchen, die in der Fruchtsaison 2000 verzeichnet wurden, waren 55% Fressbesuche von Tamarinen und 45% Fressbesuche von Totenkopfäffchen. Die Totenkopfäffchen ernteten insgesamt jedoch drei mal mehr Früchte von *L. cymosa* als die Tamarine, da sie in größeren Gruppen vorkamen (ca. 30 Individuen, gegenüber 6-9 Individuen bei den Tamarinen) und aufgrund ihrer bereits beschriebenen anderen Fresstechnik. Tamarine besuchten die Studienflächen häufiger als Totenkopfäffchen (z.B. mittleres Intervall zwischen Ernten in einer Studienfläche von 1,8 Tagen gegenüber 4,3 Tagen). Tamarine fraßen pro Besuch einer Studienfläche in weniger Bäumen Früchte als Totenkopfäffchen (z.B. mittlere Zahl der ausgebeuteten Bäume pro Besuch von 3,2 gegenüber 7,8). In den einzelnen Bäumen ernteten die Tamarine zwischen 1 und 25 Früchten pro Besuch, während die Totenkopfäffchen zwischen 1 und 224 Früchten pro Besuch ernteten. Beide Affenarten ließen in 97% aller Ernteereignisse reife Früchte in der jeweiligen Baumkrone hängen. In der Fruchtsaison von 1999 konsumierten beide Affenarten gemeinsam 9% der reifen Früchte, die von allen überwachten Bäumen zusammengenommen produziert wurden. In der Fruchtsaison im Jahr 2000 konsumierten beide Affenarten gemeinsam etwa 50% der von allen beobachteten Bäumen produzierten reifen Früchte. Der auffällige Unterschied zwischen den beiden Jahren war zum Teil darauf zurückzuführen, dass in der Fruchtsaison von 1999 30% der reifen Früchte mit Schmetterlingslarven befallen waren und von den Bäumen abgeworfen wurden, so dass sie nicht mehr für die baumlebenden Fruchtfresser zur Verfügung standen. Dagegen wurde im Jahr 2000 kein Befall von Früchten beobachtet.

- Jede meiner Studienflächen war Teil des Kern-Wohngebietes von jeweils einer Gruppe von Schwarzrückentamarinen, und fiel in das Streifgebiet einer Gruppe von Totenkopfäffchen. Die Fruchtfressergemeinschaft an einzelnen Bäumen von *L. cymosa* ist folglich klein und die Verfügbarkeit von Samenausbreitern gering.
- Die Kriterien eines „spezialisierten Samenausbreitungssystems“, wie von Howe et al. (1977) definiert bzw. zusammengefasst, sind sowohl für die Eigenschaften von *L. cymosa* erfüllt als auch für die Seite der Fruchtfresser im Samenausbreitungssystem dieses Baums. Schwarzrückentamarine sind wichtige Samenausbreiter von *L. cymosa*. Die Interaktion zwischen *S. nigricollis* und *L. cymosa* scheint eng genug, um ein Potenzial für selektive Einflüsse des Samenausbreiters auf die Fruchtmerkmale und die Merkmale der Fruchtreifung des Baums erwarten zu können.
- In einer Stichprobe von 6 Bäumen vergleichbarer und hoher saisonaler Fruchtproduktion war die Gesamtanzahl an reifen Früchten eines jeweiligen Baums, die durch den zuverlässigen Samenausbreiter *S. nigricollis* im Verlauf einer Fruchtsaison geerntet wurden, mit keinem der gemessenen Nährstoffbestandteile des Fruchtfleischs signifikant korreliert (gemessen wurden: Fruktose, Glukose, Saccharose, Gesamtprotein; das Fruchtfleisch enthält keine Lipide). Sie war ebenso nicht korreliert mit der Gesamtmenge metabolisierbarer Energie, mit dem Gewichtsverhältnis von Samen zu Fruchtfleisch und dem Wassergehalt des Fruchtfleischs. Fraßpräferenzen für einzelne Zucker, wie sie von Laborstudien ermittelt wurden, konnten in dieser Feldstudie nicht bestätigt werden. Der zuverlässige Samenausbreiter von *L. cymosa* scheint keinen Selektionsdruck auf den Nährstoffgehalt der Früchte von *L. cymosa* auszuüben.
- Die saisonale Fruchtproduktion eines *L. cymosa* -Baums war die hauptsächliche Vorhersagevariable für alle Aspekte der Fruchtentnahme durch den effektiven Samenausbreiter, *Saguinus nigricollis*, sowie auch durch den Nicht-Samenausbreiter, *Saimiri sciureus*. Bäume mit größerer saisonaler Fruchtproduktion hatten eine höhere Wahrscheinlichkeit der Fruchtentnahme durch den Samenausbreiter als Bäume mit kleinerer saisonaler Fruchtproduktion. Von Bäumen mit größerer saisonaler Fruchtproduktion ernteten die Samenausbreiter ebenfalls mehr Früchte. Diese Bäume hatten also einen größeren Ausbreitungserfolg. Der prozentuale Anteil der vom Samenausbreiter entnommenen Früchte an der gesamten saisonalen Fruchtproduktion eines Baums, also die Samenausbreitungseffizienz eines einzelnen Baums, sank jedoch

mit wachsender Fruchtproduktion. Im Gegensatz dazu stieg der prozentuale Anteil der vom Nicht-Samenausbreiter abgeernteten Früchte an der gesamten saisonalen Fruchtproduktion mit größer werdender saisonaler Fruchtproduktion. Ebenso stieg die Wahrscheinlichkeit der Fruchtentnahme durch den Nicht-Samenausbreiter und die Anzahl der von ihm geernteten Früchte mit größer werdender saisonaler Fruchtproduktion. Die beobachteten Unterschiede zwischen Samenausbreiter und Nicht-Samenausbreiter sind auf Unterschiede in der jeweiligen Nahrungsaufnahmekapazität, der Gruppengröße und des Fouragierverhaltens zurückzuführen.

- Tamarine ernteten mit geringerer Wahrscheinlichkeit *L. cymosa* Bäume, die nicht oder nur wenig von umgebender Vegetation gedeckt waren. Dies reflektiert wahrscheinlich ein Verhalten der Tamarine zur Vermeidung von Angriffen von Wald-Raubvögeln.
- Bei hoher Dichte von *L. cymosa*-Früchten in der Nachbarschaft einzelner Bäume verringerte sich der Anteil der Früchte an der saisonalen Fruchtproduktion, die von Tamarinen geerntet wurden. Dies spricht für Konkurrenz von Bäumen um Samenausbreiter.
- Meine Studie hat Selektionsdrücke der Samenausbreiter auf die saisonale Fruchtproduktion von *L. cymosa* aufgedeckt. In Übereinstimmung mit der „fruit crop size-Hypothese“ wurden große saisonale Fruchtproduktion dadurch begünstigt, dass der effektive Samenausbreiter hier mit höherer Wahrscheinlichkeit überhaupt Früchte erntete und dass er eine höhere Zahl von Früchten entnahm. Die sinkende Effizienz der Samenausbreitung bei großer saisonaler Fruchtproduktion scheint andererseits Selektion gegen hohe saisonale Fruchtproduktion auszuüben (stabilisierende Selektion).
- Meine Daten deuten darauf hin, dass auch der Nicht-Samenausbreiter Selektion gegen hohe saisonale Fruchtproduktion ausübt, indem es durch seine Fruchtentnahme zu „Verschwendung“ von Früchten kommt.
- Die „fruit crop size-Hypothese“ scheint auch für den affenverbreiteten Baum *L. cymosa* ein gültiger theoretischer Rahmen zu sein. Meine Studie hat jedoch gezeigt, dass sowohl die Wahrscheinlichkeit der Fruchtentnahme durch den Samenausbreiter als

auch die Rolle der nicht samenausbreitenden Fruchtnutzer in diesen theoretischen Rahmen mit einbezogen werden sollten. Meine Ergebnisse zeigen ebenfalls, dass es auch Faktoren außerhalb der Kontrolle eine Baumindividuums gibt, die die Fruchtentnahme von *L. cymosa* Bäumen beeinflussen. Selektion durch Samenausbreiter könnte durch Nachbarschaftsbedingungen begrenzt, jedoch nicht verhindert werden.

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Appendices

Appendix A

Content of amino acids in 13 fruits of *Leonia cymosa* collected from 10 different trees in the forest near Laguna Grande de Cuyabeno, Ecuador.

Values given in the table are µmole/g dry weight.

Calculated only from peaks that could be reliably identified.

sample no.	tree no.	ASP	THR	SER	ASN	GLU	AAAA	GLY	ALA	VAL	ILE	LEU	GABA	NH3
2	p24, yellow			1.11		3.71			1.36					5.16
19	p24, green to yellow					4.82			1.54					6.94
26	p52a1, amar			3.1		6.93		0.94	7.17	1.87	1.28	2.42	3.69	4.65
39	p52a1, green to yellow		1.11	3.44		7.3			3.38	1.52	1.49	2.89	5.91	4.02
41	pal 34								3.87					17.9
47	pal 53								3.02					6.2
63	pal 23							1.21	4.55	1.18			6.95	3.53
73	hl 63	5.1		2.71	2.58	5.16	8.42		3.13	1.91				12.8
88	Jul 54													16
93	julio 6													12.1
108	pal 6							4.23	1.8					9.43
116	sal 7	3.74	1.86	6.18		7.89		1.18	1.96	2.49				12.8
130	na 123													

Asparagine, Threonine, Serine, Aspartate, Glutamic acid, alpha-amino adipine acid, Glycine, Alanine, Valine, Isoleucine, Leucine, Gamma-amino butyric acid, Ammoniac

Appendix B

Alternative fruit sources for monkeys during fruit maturation of *Leonia cymosa* from March to May 2000 in the forest near Laguna Grande de Cuyabeno, Ecuador.

scientific name[1]	**local name (Siona name/ Spanish name)**	**fruiting season**[2]	**used by *Saguinus***	**used by *Saimiri***	**forest stratum**	**abundance (no. of trees in all study lots)**	**literature citation** [3]**: reported as food of *Saguinus* sp.**
Perebea cf. mollis (Moraceae)	Me̲’se / -	April / May	X	X	subcanopy	30	Roosmalen 1985
Couma macrocarpa Barb. Rodr. (Apocyanaceae)	Huansoca / -	April / May	X	X	subcanopy, canopy	9	Peres 1993
Parkia nitida Miq., *P. balslevii* H.C. Hopkins (Mimosaceae)	Gaj̲é / guarango	all year, only a few individuals at the same time	X		emergent	24	Izawa 1978; Peres 1993; Knogge 1999
Dialium guianense (Aublet) A.C.Smith (Fabaceae, Caesal-piniaceae)	Kayá / tamarindo	April / May	X	X	canopy	1	
Ficus sp. (Moraceae)	Ënesa / -	all year, only a few individuals at the same time	X	X	emergent	4	de la Torre 1991; Peres 1993; Knogge 1999; Pack, Henry et al. 1999
Inga sp. (Mimosaceae)	Sisi bene / guabilla	February to April	X		canopy	14	de la Torre 1991; Peres 1993; Knogge 1999; Pack, Henry et al. 1999 Garber 1986
Hymenaea oblongifolia Huber (Fabaceae)	Sojó / -	April / May	X		canopy	6	Ulloa 1988

[1] determined by Gorky Villa, Herbarium (QCA) of the Catholic University of Quito (PUCE). Leaf and fruit specimen were deposited in the herbarium of the Pontifícia Universidad Católica in Quito (QCA, specimen No. 1-16, 2001, Albrecht Pfrommer).

[2] I searched the study plots for trees fruiting at the same time as *L. cymosa* and producing fruits that were either similar in morphology to those of *L. cymosa* and/or were identified by local indigenous assistants as attractive food for *Saguinus nigricollis* and/or *Saimiri sciureus* (Victoriano Creollo, Tomás Creollo, personal communication). I also searched for trees that were named in the literature as a top food resource of *Saguinus* sp. or *Saimiri* sp. (e.g. in Izawa 1978; Terborgh 1983; Roosmalen 1985; Garber 1986; Ulloa 1988; de la Torre 1991; Egler 1992; Peres 1993; Knogge 1999; Pack, Henry et al. 1999).

[3] species or genus

References

de la Torre, S. (1991) Area de vida, comportamiento reproductivo y habitat de *Saguinus nigricollis graellsi* (Primates: Callitrichidae) en la Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 162

Egler, S. G. (1992). "Feeding ecology of *Saguinus bicolor bicolor* (Callitrichidae: Primates) in a relict forest in Manaus, Brazilian Amazonia." Folia Primatologica **59**: 61-76.

Garber, P. A. (1986). "The ecology of seed dispersal in two species of calltrichid primates (*Saguinus mystax* and *Saguinus fuscicollis)*." American Journal of Primatology **10**(2): 155-170.

Izawa, K. (1978). "A field study on the ecology and behavior of the Black-mantle tamarin (*Saguinus nigricollis*)." Primates **19**(2): 241-274.

Knogge, C. (1999). Tier-Pflanze-Interaktion im Amazonas-Regenwald: Samenausbreitung durch die sympatrischen Tamarinarten *Saguinus mystax* und *Saguinus fuscicollis* (Callitrichidae, Primates). Münster, Schüling Verlag.

Pack, K. S., O. Henry, et al. (1999). "The insectivorous-frugivorous diet of the golden-handed tamarin (*Saguinus midas midas*) in French Guiana." Folia Primatologica **70**: 1-7.

Peres, C. A. (1993). "Diet and feeding ecology of saddle-back (Saguinus fuscicollis) and moustached (S. mystax) tamarins in an Amazonian terra firme forest." J. Zool., Lond. **230**: 567-592.

Roosmalen, M. G. M. v. (1985). Fruits of the Guianan flora. Utrecht, Utrecht University: Institute of Systematic Botany.

Terborgh, J. (1983). Five new world primates: a study in comparative ecology. Princeton, Princeton University Press.

Ulloa, R. (1988) Estudio sinecologico de primates en la Reserva de Producción Faunistica Cuyabeno, Amazonia Ecuatoriana. Tesis de licenciatura, Departamento de Ciencias Exactas, Pontificia Universidad Catolica del Ecuador, Quito, pp 179

Appendix C

Fruit quality of six trees of *Leonia cymosa* with large fruit production, and fruit removal in these trees by black mantle tamarins, *Saguinus nigricollis*, in the forest near Laguna Grande de Cuyabeno, Ecuador. Nutrient content values are medians from ten fruits sampled per tree.

Tree	**Seasonal fruit crop size**	**Number of fruits removed**	**Proportion removed**	**Number of harvest events**	**Fructose (mg/g dry weight)**	**Fructose Concentration (%)***	**Glucose (mg/g dry weight)**	**Sucrose (mg/g dry weight)**	**Sucrose Concentration (%)***	**Total sugar (mg/g dry weight)**	**Protein (mg/g dry weight)**	**Water content (% fresh weight)**	**Pulp fresh weight / seed fresh weight**	**Energy (kJ/g dry weight)**
p23	255	83	32.5	8	201.8	8.2	231.5	161.8	5.0	607.9	161.6	74.6	1.2	13.1
p24	289	22	7.6	3	193.6	6.7	230.3	183.6	6.2	586.3	177.1	74.4	1.1	13.0
p34	216	15	6.9	1	248.7	8.9	275.3	79.2	3.7	641.7	235.3	71.4	0.8	14.9
p52a1	173	34	19.7	5	97.0	3.9	134.2	361.3	14.8	598.8	128.6	72.6	1.7	12.4
p53	107	17	15.9	5	165.5	5.7	193.5	132.1	3.9	481.4	193.2	73.2	1.1	11.5
p06	94	0	0	0	166.9	4.0	174.6	13.6	0.3	369.6	189.5	80.5	1.2	9.5

* % solution (weight/volume)

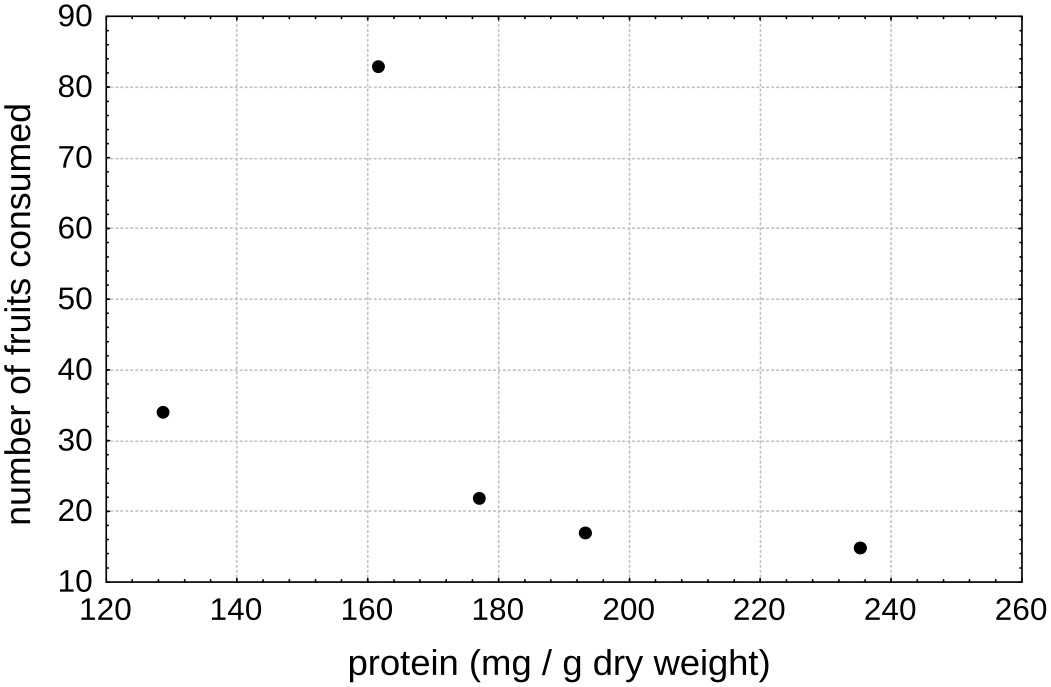
Appendix D

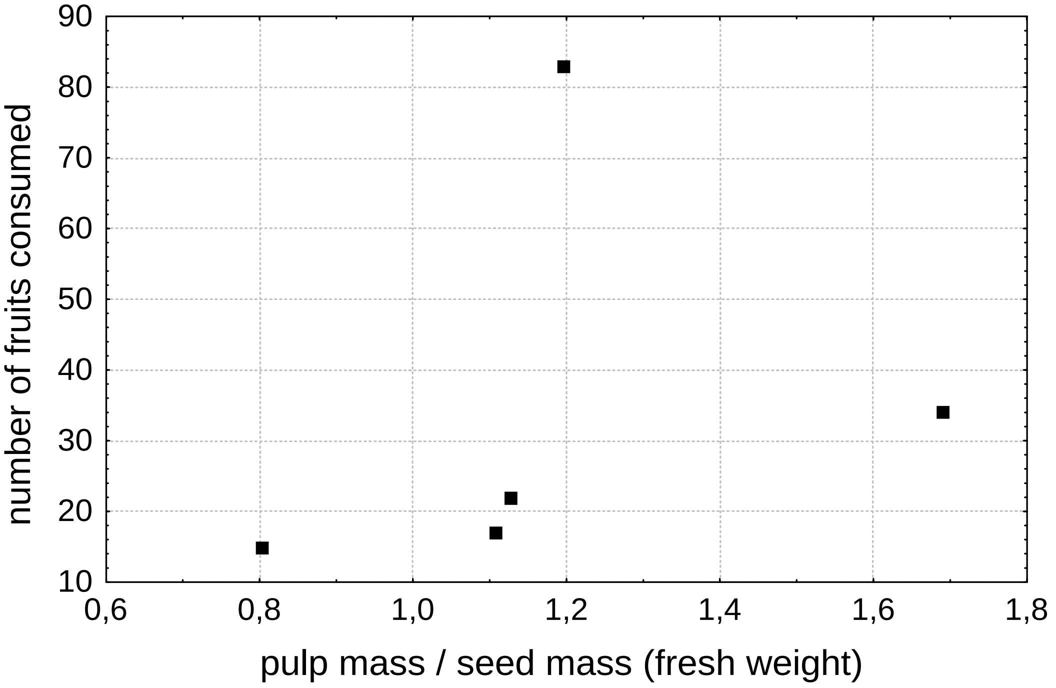
Correlation matrix of median fruit nutrient contents of five trees of *Leonia cymosa* from the forest near Laguna Grande de Cuyabeno, Ecuador (Spearman's R values, *p<0.05, ***p<0.001)

	Glucose	Sucrose	Total sugar	Protein	Water	Energy	Pulp/seed ratio	Seasonal fruit crop size
Fructose	1.0 ***	- 0.7	0.7	0.6	0.0	0.9 *	- 0.6	0.5
Glucose		- 0.7	0.7	0.6	0.0	0.9 *	- 0.6	0.5
Sucrose			- 0.3	- 0.9 *	0.3	- 0.4	0.9 *	0.2
Total sugar				0.1	- 0.3	0.9 *	- 0.1	0.3
Protein					- 0.4	0.3	- 1.0 ***	- 0.1
Water						- 0.1	0.4	0.5
Energy							- 0.3	0.6
Pulp/seed ratio								0.1

Appendix E

Significant single correlations of fruit consumption by *Saguinus nigricollis* with a) pulp mass to seed mass ratio (R = -0.9; t(n-2) = -3.576; p =0.04), and b) protein content of the fruit pulp (R = 0.9; t(n-2) = 3.576; p = 0.04), in five trees of *Leonia cymosa* in the forest near Laguna Grande de Cuyabeno, Ecuador.





Appendix F

GLM summaries and Spearman correlations summarized in Table 1, chapter 4.2:

<u>Glossary of variable names:</u>

Produktion	Seasonal fruit crop size (no. of ripe fruits)
hoehe	Tree height (m)
synchro.abweich	Synchrony of fruit maturation with con-specifics trees; deviation of the peak of fruit maturation from the median peak of fruit maturation of all trees monitored (in days)
proz.frei	Percent covering of the peripheral area of the tree crown by surrounding vegetation
ernt.tam.bin	Harvest by *S. nigricollis* (0 / 1)
Ernt.tam	Number of ripe fruits removed *S. nigricollis* throughout the season
left.tam	Number of ripe fruits not removed by *S. nigricollis*
ernttam.perc	Proportion of fruits removed by *S. nigricollis* (obtained by **R**-procedure “cbind ( )”)
ernt.sai.bin	Harvest by *S. sciureus* (0 / 1)
Ernt.sai	Number of fruits removed by *S. sciureus* throughout the season
left.sai	Number of ripe fruits not removed *S. sciureus*
erntsai.perc	Proportion of fruits removed by *S. sciureus* (obtained by **R**-procedure “cbind ( )”)
resid or residuen	model residuals

Probability of fruit removal by *S. nigricollis*

Model summary:

```
glm(formula = ernt.tam.bin ~ Produktion, family = binomial)

Deviance Residuals:
   Min      1Q  Median      3Q     Max
-1.976  -1.093   0.609   1.074   1.337

Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.400035   0.356936  -1.121   0.2624
Produktion   0.016535   0.006793   2.434   0.0149 *
---
Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 116.23  on 85  degrees of freedom
Residual deviance: 106.53  on 84  degrees of freedom
AIC: 110.53
```

Correlation of residuals:

```
Spearman's rank correlation rho

data:  resid.tam.2 and proz.frei
S = 134289, p-value = 0.01319
alternative hypothesis: true rho is not equal to 0
sample estimates:
       rho
-0.2669396
```

Probability of fruit removal by *S. sciureus*

Model summary:

```
glm(formula = ernt.sai.bin ~ Produktion + hoehe, family = binomial)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.2832  -0.9238   0.5548   0.8127   1.9262

Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.971732   0.949680   2.076  0.03787 *
Produktion   0.026321   0.008713   3.021  0.00252 **
hoehe       -0.380515   0.151256  -2.516  0.01188 *
---
Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 109.937  on 85  degrees of freedom
Residual deviance:  91.533  on 83  degrees of freedom
AIC: 97.533
```

Correlation of residuals:

```
Spearman's rank correlation rho

data:  resid.sai and proz.frei
S = 113593, p-value = 0.5112
alternative hypothesis: true rho is not equal to 0
sample estimates:
        rho
-0.07168406
```

Number of fruits removed by *S. nigricollis*

Model summary:

```
glm(formula = Ernt.tam ~ Produktion, family = quasipoisson)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-5.1436  -3.1485  -1.2946   0.7958   8.8489

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept) 2.180018   0.197753  11.024 1.26e-14 ***
Produktion  0.004241   0.001184   3.582 0.000806 ***
---
Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

(Dispersion parameter for quasipoisson family taken to be 12.94514)

    Null deviance: 641.64  on 48  degrees of freedom
Residual deviance: 512.88  on 47  degrees of freedom
AIC: NA
```

Correlation of residuals:

```
Spearman's rank correlation rho

data:  residuen and proz.frei
S = 22449, p-value = 0.3179
alternative hypothesis: true rho is not equal to 0
sample estimates:
       rho
-0.1453407
```

Number of fruits removed by *S. sciureus*

Model summary:

```
glm(formula = Ernt.sai ~ Produktion + synchro.abweich, family =
quasipoisson)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-6.8089  -2.7628  -0.8556   1.4898   7.2988

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)      2.341504   0.130277  17.973  < 2e-16 ***
Produktion       0.008841   0.000482  18.341  < 2e-16 ***
synchro.abweich -0.028845   0.009527  -3.028  0.00377 **
---
Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

(Dispersion parameter for quasipoisson family taken to be 10.18547)

    Null deviance: 3153.88  on 56  degrees of freedom
Residual deviance:  573.91  on 54  degrees of freedom
AIC: NA
```

Correlation of residuals:

```
Spearman's rank correlation rho

data:  residuen and proz.frei
S = 31921, p-value = 0.7984
alternative hypothesis: true rho is not equal to 0
sample estimates:
        rho
-0.03450686
```

Proportion of fruits removed by *S. nigricollis*

Model summary:

```
> ernttam.perc<-cbind(Ernt.tam,left.tam)

glm(formula = ernttam.perc ~ Produktion, family = quasibinomial)

Deviance Residuals:
   Min      1Q  Median      3Q     Max
-5.385  -2.836  -1.046   1.616   9.023

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.026679   0.247140  -4.154 0.000137 ***
Produktion  -0.003752   0.001540  -2.437 0.018649 *
---
Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

(Dispersion parameter for quasibinomial family taken to be 13.27023)

    Null deviance: 688.95  on 48  degrees of freedom
Residual deviance: 596.34  on 47  degrees of freedom
AIC: NA
```

Correlation of residuals:

```
Spearman's rank correlation rho

data:  residuen and proz.frei
S = 20573, p-value = 0.7341
alternative hypothesis: true rho is not equal to 0
sample estimates:
        rho
-0.04964417
```

Proportion of fruits removed by *S. sciureus*

Model summary:

```
> erntsai.perc<-cbind(Ernt.sai,left.sai)

glm(formula = erntsai.perc ~ Produktion, family = quasibinomial)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-10.2908   -2.7489    0.7411    2.7485    6.7495

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.061096   0.203953  -5.203 3.00e-06 ***
Produktion   0.006388   0.001169   5.464 1.16e-06 ***
---
Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

(Dispersion parameter for quasibinomial family taken to be 14.61273)

    Null deviance: 1390.46  on 56  degrees of freedom
Residual deviance:  859.46  on 55  degrees of freedom
AIC: NA
```

Correlation of residuals:

```
Spearman's rank correlation rho

data:  residuen and proz.frei
S = 29608, p-value = 0.7644
alternative hypothesis: true rho is not equal to 0
sample estimates:
       rho
0.04043722
```

Erklärungen

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Ich habe diese Dissertation weder in gleicher noch in ähnlicher Weise in einem anderen Prüfungsverfahren vorgelegt.

Ich erkläre ferner, dass ich bisher noch keinen weiteren akademischen Grad erworben oder zu erwerben versucht habe.

Kelkheim, den 12.5.2009

Albrecht Pfrommer