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Feeding ecology and seed dispersal by *Ateles hybridus*, *Alouatta seniculus* and *Cebus albifrons* in a fragmented area at San Juan del Carare, Colombia

Ecology of a monkey community in a fragment

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Abstract

In Colombia, habitat disturbance and fragmentation due to human activities are major threats to biodiversity. Primates are very sensitive and are often being confined to small patches in formerly extensive forests. This is especially true for *Ateles hybridus,* a taxa identified as critically endangered and the major target of this project. With the aim to study the effects of habitat fragmentation on a monkey community, the feeding behaviour and seed dispersal of the sympatric *A. hybridus, Alouatta seniculus* and *Cebus albifrons* was assessed in a fragmented (isolated) forest with a high density of primates, in a cattle ranch in the Middle Magdalena, Colombia, in order to assess the way they are adapting to adverse conditions in terms of food and habitat availability. Scan sampling methods were used to collect systematic data, focused on describing activity budgets, diet, and home range of the species studied, as well as seed dispersal patterns. *A. hybridus* plays a major role in forest dynamics due to the quantity and variety of the seeds it disperses. Although all three sympatric species are present in this small fragment, they are showing different activity patterns and feeding preferences, experiencing overlaps in their area and feeding resources, and sharing intensely used habitat areas where there is an overuse of feeding resources. Therefore the three species of monkeys are experiencing scramble competition, where it is possible that the fruits are the limiting factor. All those findings together could rescue the long-term survival and viability of these primates.

Key words: *Ateles hybridus, Aluoatta seniculus, Cebus albifrons,* fragmentation, feeding behavior, diet, activity budgets, seed dispersal, scramble competition.

Contents

Introduction

Study species

This study was based on two members of the Atelinae subfamily: *Ateles hybridus* and *Alouatta seniculus*, and one member of the Cebidae: *Cebus albifrons*. *Ateles species* are specialized highly frugivorous (Di Fiore *et al.* 2008), while *Cebus* and *Alloutta* species are consider as a opportunistic or non-restricted frugivores, defined by Wehncke & Dominguez (2007) as "animals for which fruits do not represent the main bulk of their diet".

Ateles species has a highly frugivores diet, but is complemented in a lesser proportion by leaves, flowers, seeds, aerial roots, palm hearts, and rarely by invertebrates (as caterpillars, bees and termites), fungi and decayed wood (Di Fiore at al. 2008). They can feed on a wide array of fruiting trees and swallow their seeds dispersing it away form the parental tree (Link & Di Fiore 2006). This species are characterized by a fission-fusion strategy, where the troop loose social association along the day in smaller sub-groups, in order to get the feeding resources, this allows them to visit many trees with small crops, spending less time per feeding tree and thus dropping less fruits and seeds under the parent tree (Andresen 1999), this is associated with high metabolic rates, and as a result large home ranges in order to fulfill their energy needs (Link & Di Fiore 2006).

Aloutta species live in cohesive groups, that varies between 4-9 individuals (Andresen 1999; Wehncke *et al.* 2004), mainly vegetarian and despite appear to be the most folivorous from the New World primates, fruits can represent a large part of their diet (Julliot & Sabatier 1993). Since they are highly folivorous, they have a low metabolic rates and therefore small home ranges (Posada *et al.* 2007) with a seasonal increase on fruit consumption on periods of peak production (Andresen 1999). *Aloutta* spp. use fruiting trees that provides them enough food for the entire troop, where they spend most of the time feeding and resting (Andresen 1999).

Cebus species has troops that can vary between 10-15 individuals, has a broad diet: fruits, shoots, small vertebrates, eggs and arthropods (Wehncke & Dominguez 2007). Evidence that *Cebus* spp. are considered as important disperses is provided by Whencke & Dominguez (2007) and Wehncke *et al.* (2004), who investigated the seed dispersal of *C. apela* and *C. albifrons*, in Iguazú and Panamá. Their results showed that this species of monkey have short gut passages, therefore high rates of defecation with scatter depositions of the dung, and low time per feeding tree. This species, have big home ranges, which allow them to move the seeds far from the mother tree. Finally, despite this monkeys are not restricted frugivores; they feed upon a high diversity of fruits, without any kind of restriction.

Seed dispersal by primates

In the tropics there is a high diversity of frugivorous bird and mammal species as a result of co-evolution between fruit-eating species and the fruits they feed on (Theodore et al. 1987). Consequently, frugivores are very important for the maintenance of tropical forests diversity, if they were removed it has been estimated that as much as 60% of the species of fruiting trees could be lost, especially because most tree species benefit in recruiting the seedlings far away from their parental trees, and this role is played by a large proportion of seed dispersers (Chapman & Chapman 1995).

There are fruits which show dispersal syndromes restricted to mammals, characterized by large and protected dusk fruits, primates disperse seeds by endozoochory, syndromes for birds are related to small and non-protected fruits. As opposed to birds, primates feed on both kinds of fruits, thus, the primates' ecological role on the ecosystems is remarkable since many plants would be prone to disappear with the absence of the monkeys (Link & Stevenson 2004). A specific study with *Virola calophylla* at Peru showed that their fruits were dispersed by wide diversity of birds and on monkey's species (*Ateles paniscus*), the monkeys were found as more important dispersers than the birds, and since they removed more seeds (Russo 2003).

Primates are one of the major frugivorous groups in the Neotropics, with a significant biomass (kg/km^2) in relation with the seeds dispersed (seeds/km^2/day). This group of animals relies on a taxonomically diverse set of fruiting plants, and has a considerable ecological influence on the forest, playing a key role in its regeneration and dynamics (Chapman 1995; Lambert & Garber 1998; Link & Di Fiore 2006).

Seed removal and dispersal is the first step for the colonization, establishment and further recruitment of a plant. Spatial patterns of seed dispersal play an important role in the structure and local history of the forest (Lambert & Garber 1998; Russo & Augspurger 2004). Seeds dispersed far away from the parental tree and with scatter distribution have a greater chance of succeeding and lesser risk of predation than those fallen underneath tree crowns of the parental tree and with clumped distribution, this ones has less probability of being recruited into a seedling (Janzen 1970; Chapman & Chapman 1995; Chapman 1995; Russo & Augspurger 2004).

Effectiveness of the seed dispersal

Atelinae, a subfamily composed by *Ateles* spp., *Alouatta* spp. and *Lagothrix* spp., appear to be the primary vertebrate seed dispersers of plants in the Neotropics, partly due to their handling of the seeds, since they do not damage the seeds consumed (Stevenson *et al.* 2001). From the three Atelinae, *Ateles* spp. are considered as the most specialized frugivorous, followed by *Lagothrix* spp. Both of them complement their diet by eating leaves, and finally *Aloutta* spp. which mainly eats leaves but also a high proportion of fruits (Stevenson *et al.* 2002; Lawrence 2005). *Ateles* spp. have the ability to feed on a wide range of fruiting species (Link & Di Fiore 2006), and as Lawrence (2005) found in a study carried out in Ecuadorian Amazonia with *A. belzebuth*, some fruit species are almost exclusively consumed by them.

Primate's species show different seed dispersal patterns, both at spatial and temporal scales (Zhang & Wang 1995). In Africa, studies have shown that seeds of many plant species are not able to germinate under the parent tree, or that most seeds and seedlings are predated by predators or parasites, plants thus relying on primate seed dispersal for their survival (Chapman & Chapman 1995; Chapman 1995). Similarly, in Perú a study focused on *Virola callophyla* by Russo & Augspurger (2004) showed that *Ateles paniscus* influences the recruitment patterns of the plant, by enhancing the survivorship of the seeds, due to a positively correlation between the density of the seeds dispersed and the travelling distance of the animals.

For the dispersal events, the dispersal effectiveness depends both on the quantity and quality of the dispersed seed. Quantity is related to the total number of seeds removed per visit on a feeding tree. Quality depends on the treatment the seeds receive (in mouth and gut), density of seed deposition, and seed survival and subsequent seedling growth (Schupp 1993).

In Colombia, Stevenson *et al.* (2001) compared the germination rates of the seed dispersed by the three Ateline monkeys (*Ateles. belzebuth*, *Lagothrix lagotricha* and *Alouatta seniculus*) with the control seeds. They found that the monkeys do not have a strong effect on the quality of the dispersed seed, due to the effects on germination were neutral (*A. belzebuth*) or slightly positive and neutral (for *L. lagotricha* and *A. seniculus*). Despite the lack of differences between the germination rates of seeds dispersed by *A. belzebuth* and the control ones, it was established that these monkeys are the most efficient dispersers, since dispersed more seeds.

Ecological role of primates

The importance of primates as fruit eating species relays on the fact that they do not decrease the viability of the seeds in the fruits they eat. Lawrence (2005) found that *A. belzebuth* preys the seeds of only *Iriartea deltoidea*, from 64 plant fruiting-plant species on their diets. Similarly, from 152 fruit species consumed by *A. belzebuth,* Link & Di Fiore (2006) found that they pry on *Socratea exorrhiza* and *Psudolmedia laevis,* and Andresen (1999) found no predation upon the handled seeds, nor for *A. paniscus*, neither for *A. seniculus*, from 71 and 14 fruiting-plants consumed from each monkey species respectively.

When studying the seed dispersal of *A.belzebuth* in Ecuador, Link & Di Fiore (2006) found that this monkey moves a large number of seeds, due to high defecation rates along the day, due to the need to discharge indigestible food. In the same way they found that *A.belzebuth* can disperse the seeds over long distances, and away form the mother tree. This trait is associated with their social structure, characterized by large groups and the fission-fusion group strategy.

Comparing the feeding ecology and seed dispersal between *C. capucinus* and *A. palliata*, it was found that the former consumed more species of fruits (33 vs. 10) and deposited a greater percentage of feces with seeds (98% vs. 54%). However *C. capucinus* consumed mainly small-seeded fruits (up to 1.5 cm), while *A. palliata* fed on fruits of bigger size (up to 2.5 cm) (Wehncke *et al.* 2003).

Comparing the feeding ecology and seed dispersal between *A. paniscus* and *A. seniculus,* it was found that *A. paniscus* swallowed and dispersed seeds of 71 plant species, while *A. seniculus* fed and dispersed 14 plant species. *A paniscus* move more seeds number on the total fecal samples, from 47 feces 2086 seeds were collected, from 27 fecal samples 269 seeds were collected for *A. palliata* (Andresen 1999). Similarly, Stevenson *et al.* (2002) found that *A. belzebuth* fed on 83% of the fruiting species, while *A. seniculus* consumed 53% of them. In terms of defecation times, Whencke *et al.* (2004) found that troops of *Alouatta* spp. use to defecate at the same time twice a day, early morning and before the end of the day, in contrast Link & Di Fiore (2006), studying *A. belzebuth* found that the species defecated on average 13.7 times per 12 h, almost one defecation per hour per day.

Comparing between tree sympatric species, *C. capucinus, A. palliata* and *A. geoffroyi*, the first species has the shortest retention times of the three, with 1.7 h, 20.4 h and 4.4 h respectively; this means that *Cebus* species has higher defecations rates per day with lower amount of seeds per deposited feces.

As the resource segregation is different in these three sympatric species groups, is the main reason why it is important to study behavioral ecology of these species, with resource limitations as is one of the aims of the present project.

In general terms, between populations of arboreal species, it is possible to see competition by the sites and resource. Zhang & Wang (1995), found a higher competition between individuals of the same troop in *Cebus*, and Andresen (2002) found *Alouatta* are easily displaced from the fruiting trees by spider monkeys.

Aloutta and *Ateles* species characteristically swallow large-sized seeds. Link & Di Fiore (2006) in a study carried out at Ecuador, found in the 95% fecal samples of *A. belzebuth,* seeds greater than 3mm (>3mm). Similarly Andresen (2002) in Brazil found in most of the feces of *A. seniculus* seeds bigger than 3mm. Some of the large-seeded plants rely on the monkeys as primary seed disperser, since their seeds can not be optimally handled by other animals. Thus, the decreasing primate populations, together with the habitat loss, make those plants more prone to the extinction (Cramer *et al.* 2007).

Effects of habitat fragmentation

In spite of the important role primates play in the tropical forest ecology, they are facing the effects of both, habitat loss (especially large-bodies primates) and unsustainable hunting (Peres 2001). The consequences of the habitat loss are fragmentation, discontinuity and isolation once the deforestation has reached the higher levels (Cowlishaw & Dunbar 2000).

It has been generally stated that, the loss of seed dispersers will be reflected in loss of fruiting trees. The loss of trees is the result in a reduction of diversity; density and distribution of seedlings, given most of the fruits eaten by primates are unavailable for other frugivorous. With this disruption, the ecological interaction and behavioral ecology would affect the forest community and dynamic, threatening the long term persistence of the tropical ecosystems (Chapman 1995; Chapman & Chapman 1995; Garber & Lambert 1998; Chapman & Onderdonk 1998; Cramer *et al.* 2007).

Another of the implication with the forest fragmentation, are the problems associated with microhabitat changes. This is related with the effects of higher wind exposure and ambient temperature, as well as reduced humidity especially in the forest edges. The result is an increase in tree mortality, damage and formation of canopy gaps. Such changes can bring an increase in plant species adapted to gaps and disturbed areas (pioneers). Consequently, a decrease in old-growth canopy trees (Cowlishaw & Dunbar 2000; Norconk & Grafton 2003).

In the same way, it has been shown by Cramer *et al.* (2007), that the large seeded-plants reduce their population in fragmented forest. Large-seeded trees are almost inaccessible for frugivorous as birds or small mammals, being limited from medium to large mammals (as Atelines group) for the handling of their fruits. This resulted on a highly specialized association between plant and seed dispersers.

Since forest and frugivorous population decline is a fact, it is important to understand the role of primate seed dispersal (feeding ecology) and the interaction with the plants sustain them. Understanding the animal-plant ecological interaction provides valuable tools for conservation, in order to generate adequate policy decisions regarding with both primates and forest management and preservation (Chapman 1995; Garber & Lambert 1998; Lawrence 2003).

The current study will help us to better understand the negative impacts of the continuing habitat loss in the monkey's wild populations. This is particular important for the conservation of *A. hybridus,* as they have been proposed to be one of the first taxa to potentially go extinct due to habitat degradation and human intervention in Colombia.

Studying the effects of the forest fragmentation, provide the first steps to understand how to generate in the future conservation and management practices in order to guarantee a better fate for the species. Despite the isolated areas provide a refugee for certain species; it is important to have in mind that isolated species will face long term viability problems on its populations. Since most of the forest in Colombia are facing the effects of habitat loss, becoming small fragments that can be or not isolated, study the feeding ecology and seed dispersal of this community in the fragmented and isolated forest at San Juan, can provide the first steps to understand how the primates communities are being affected in a general way, as well as how they are adapting or answering to the new conditions, and consequently generate conservation initiatives for the long term conservation of both, the animals and their forests.

For that reason this study was developed with the aim to describe the feeding ecology and the seed dispersal patterns, of the sympatric *A. hybridus, A. seniculus* and *C. albifrons* in an isolated forest at San Juan del Carare-Colombia, with a high density of primates in a small area. This allow us to understand the way how they answer towards a limited factor as could be the feeding resources, which in the same way could affect the long term survival of the species at the study area.

Objectives

General Objective

The main objective of this research project is to describe the feeding behavior and the seed dispersal patterns of a primate community in the fragmented forests at San Juan de Carare, Colombia.

Specific Objectives

1. Diet and inter-specific feeding competition in the primate community at San Juan de Carare.
    a. Describe the feeding strategies and diet of sympatric *Ateles hybridus*, *Alouatta seniculus* and *Cebus albifrons* in forest fragments with very high primate density.
    b. Establish the competitive regime for the local primate community, in terms of dietary overlap (scramble competition).
    c. Evaluate the feeding strategies of the primate community.
    d. Describe the activity budgets of the species; to general understand their feeding behavior.
2. Investigate the role of the primate community of seed dispersal.
    e. Identify the plants dispersed by each primate species in San Juan del Carare.
    f. Describe the temporal and spatial seed dispersal patterns of the primate community

Methods

Study area

The study area is located in a private cattle ranch called "Hacienda San Juan del Carare" located in the San Juan River in the middle Magdalena, Cimitarra Region, Santander department, in Colombia. The study site is located aprox. 10 km from the Magdalena river on its Eastern bank, in Bocas del Carare between Puerto Berrío and Barrancabermeja (Fig. 1). The forest is a tropical rain forest (Humboldt Institute 1998), which is between the 150-200 meters above the sea level. The area follows the regime winter patterns of the Country, with two marked rainy periods, the first one from March to May, and a second one from October to November, with an annual medium rainfall of 3496.5 mm, medium temperature of 27.9 °C and a medium humidity of 80%. (IDEAM 2007).

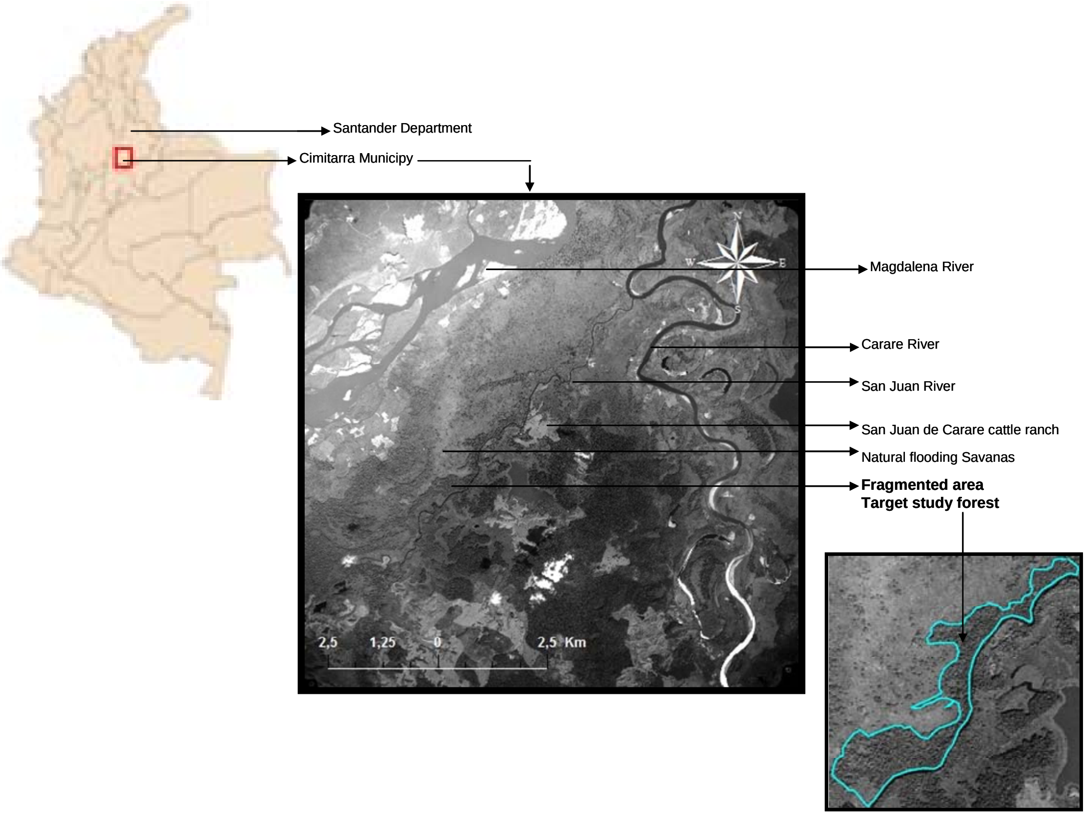

Figure 1. Geographical location of the study area at San Juan del Carare in Colombia, and the fragment of forest were the study was conducted. The soil of the study area is acidic with high contents of aluminum and low quantities of calcium and phosphorus, and is not used for agriculture or forestry "Villanueva, B & Link A. pers. comm.".

The area is characterized by the presence of forests with different degrees of fragmentation, surrounded by recently transformed pastures used for cattle ranching. The study area is located adjacent to the Magdalena River, the main river in Colombia, which receives a large amount of water from the eastern and central mountains. During the rainy seasons, most of the water is accumulated and as a result some of the areas get flooded for several weeks or months (Fig. 2). A large part of the remaining forests are wetlands or swampy areas not suitable for other economic activities.

Figure 2. Forest at San Juan de Carare, Colombia. Flooding areas in different trail system used for the monkeys followings. The circles in the photo are indicating the flagging mark of the reference trees in the trail. Photo: Proyecto Primates Colombia.

The study was carried in one of the forest fragments, located on a seasonally flooded area. The fragment is located to the East, of the forest border with the Rio San Juan. On the South and North the forest is surrounded by cattle grazing areas, and on the west there are natural flooding savannas. This is an isolated fragment, where the primate community may face a certain degree of competition not only for space but also for feeding resources. The particular conditions in this forest fragment (high primate density and low resource availability) set an ideal opportunity to study the feeding and behavioral adaptations of primates to human intervention.

The forest became an isolated fragment as a result of the forest cutting for cattle ranching, activity that began from the last 20 years approximately. Before these activities occur, the fragment was a continue forest that stretched along the San Juan River (Fig. 1). The forest is not characterized by pioneer species, since most of the plant species DBH higher than 10 cm, but by species that already represent forest coverage characteristic of the tropical rain forest "Villanueva, B & Link A. "Villanueva, B & Link A. "Villanueva, B & Link A. pers. comm.".

In order to estimate the extent of the forest, an aerial photo from 1994 and the Cartography of the Area was obtained from the IGAC (Geographic Institute Agustín Codazzi, in spanish, Instituto Geográfico Agustín Codazzi). The aerial photo was geo-referenced based on the cartography of the area with ArcMap 9.2. With this it was possible to estimate the extent of the area, locate the trail system upon the study forest and measure the dispersal distances of the monkey species. The studied fragment has an area of 65,87 ha (Fig. 1), and has a trail system to follow animals. The trail system is based on one main trail (Ar), and 7 secondary trails (Br-Ir) (Fig. 3). The trail system was already mapped, and has reference points located each 25m.

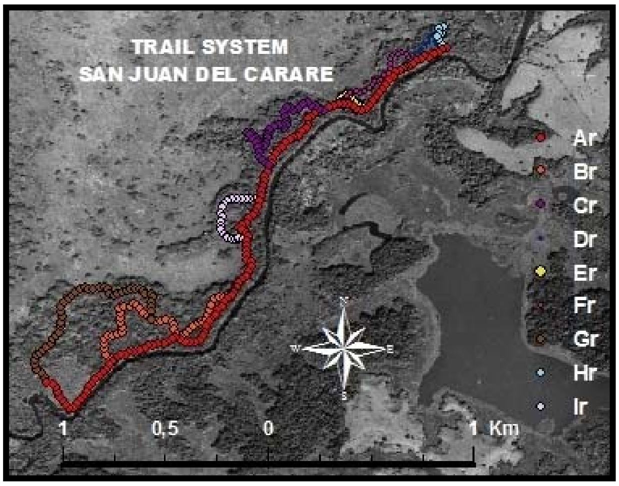

Figure 3. Trail system for the followings of the primates at the forest fragment in San Juan del Carare, Colombia. Comprises a main trail (Ar) and eight secondary trails (Br-Ir).

Study primates

There are four different species of primates, not only in the studied forest but also in the adjacent forest. There are three diurnal apecies: Brown spider monkeys (*Ateles hybridus),* red howler monkeys *(Allouatta seniculus)*, white headed capuchins (*Cebus albifrons)* and one nocturnal owl monkeys (*Aotus* sp.). A diverse mammal species and birds are also found in the study area, these can play an important role as seed disperses in the area. From mammals there is presence of terrestrial frugivorous as *Dasyprocta* sp, *Sciurus* sp, *Eyra barbara,* this last one is mainly omnivorous but also eats fruits on high proportion. *Aotus* sp., and bats, represents frugivorous arboreal mammals. There is also presence of frugivorous birds on the area, (e.g. members of the Thraupidae, Pipridae family and pava). These species, together with the presence of folivorous species as *Bradyptus variegatus,* would imply more competence for the feeding resources in the area.

There are two social groups of spider monkeys present in the forest fragment, one of them is well-habituated (named SJ1) and the individuals and social structure are well-known (Table 1). There are many groups of howler, three of them are identified and categorized in three different groups (A, F, N).

Table 1. Group composition of one of the A. hybridus study group (Named SJ1).

Gender	Age	Number
Male	Adult	5
	Sub-adults	1
	Juvenile	2
Females	Adults breeding	4
	Adults	4
	Sub-adults	1
	Juveniles	3

From the diurnal primate species at San Juan, *Ateles hybridus* is an important conservation target, and it has been classified as critically endangered by the International Union for Conservation of Nature (IUCN), principally because of the habitat fragmentation but also for hunting impact. During the last five years they have been categorized as one of the 25 most endangered species on the planet. Despite its category, the species is poorly known, and only one long term study is being conducted to describe its behavioral ecology and population biology in the wild. This study is a part of "Proyecto Primates" conservation and research initiative carried out at Serranía de las Quinchas and San Juan del Carare in Colombia.

This study focuses on the three diurnal primate species (Fig. 4), due to the "adverse" conditions they are living in.

Activity budgets

Scan sampling

In order to determine the time spent by each species in different activities (Table 2), we recorded the activities using scan sampling methods (Altmann 1973). Every five minutes, the behavioral activity of all individuals that were in sight of the observer was registered for approximately 10 s.Whenever possible the observations were taken from 06-hour clock to 18-hour clock, from Monday to Saturday. One hour comprises of 12 scan samplings and one observation day of 144 scans samplings

Figure 4. Monkey community present at San Juan del Carare, Colombia. A. A. hybridus (eating leaves). B. A. seniculus., and C. C. albifrons. Photo: Proyecto Primates Colombia.

The data register of the scans was not always continuous, since the animals could be out of sighting. Every scan was finished if the animals were out of sight for more than 20 minutes. In the same way, with the flooding of the forest and the rainy season (October- mid December) it was not possible to carry out continuous followings every day. For the three monkey species data were collected from June 2008-February 2009.

Table 2. Description of the Behavioral categories registered during the primate follows with the scan sampling methods at San Juan del Carare, Colombia.

Category	Description
Feeding	Individuals are eating any part of the plant or some other resource. Sub-activities: Feeding time on fruits, leaves, wood, flowers, and on seeds and foraging (for this purpose is defined as the manipulation of the substrate in order to get food, mainly but not necessarily insects, this category is used for *C. albifrons* since they use to eat insects).
Movement	Evident change on the position of the animals. It can be either on the same tree or trough the canopy in the forest
Rest	Activity when the animals are calm, stationary or sleeping
Social Activity	Activity when the individual of the group are interacting
Other	Includes events of defecation or other non-social activities

Scan sampling analysis

The scans are considered as independent events, therefore the activity budgets are obtained as a percentage. The percentage of the activity was obtained as follows: % activity = $(n_1*100)/N$. Where n_1 is the number of scans in which each activity was recorded and N is the total number of scans. Percentages of the activities were obtained for each species.

With the purpose to establish the feeding strategies and inter-specific feeding competition, a histogram with the frequencies of feeding behavior along the day was done, in order to assess differences on the feeding time between the species as well as resource segregation.

Chi-square tests were conducted in order to compare between the three species if there were differences between the time periods of each of the behavioral categories. A separate chi-square test was also done in order to find if there were differences or not in the type of feeding item between the evaluated three monkey species.

Primate feeding behavior

Feeding bouts

In order to describe the feeding strategies and diet of the primate community at San Juan, behavioral follows were conducted for all species in the forest fragment. Whenever possible, for each scan sample, the feeding bouts were calculated. A feeding bout is the time the monkeys are feeding on a plant, and counts from the moment the first individual starts feeding and ends when the last individual leaves the feeding tree or liana. During feeding bouts the type of item consumed (e.g., fruits, flowers) by the species was recorded. For a description of the methods see annex one.

Feeding bout analysis

Total feeding time for each species per month and for the entire study period was calculated from feeding bouts data. Percentage of time spent on each feeding resource (explained further) was calculated from the total feeding time. The percentages of the feeding time are presented for each month and for the entire study period. In the case of *A. hybridus* it was possible to get data from June 2008 to February 2009, but for *C. albiforns* and *A. seniculus* data are from December 2008 to February 2009 only. Comparisons between the species are presented for those months where data are available for the three of them. Additionally, *A. hybridus* was analyzed separately, to estimate its total feeding behavior along the study period.

The bias on the feeding bouts relays in that most of the observations were based on the feeding behavior of *A. hybridus*, there were not enough data for the feeding bouts of *C. albifrons* and *A. seniculus*. The main reason is because is the target species to study, not only because of its threatened category but also because there is not studies already conducted on this species.

Dietary preferences for the monkey community estimated from feeding bouts

A species comparison on plant species consumed could not be made, because for *C. albifrons* and *A. seniculus* the registers of the plant species they fed on are very small, since most of the plant species were not identified, not only for lack of knowledge of the field assistants but also because some plant species are still in identification process.

Analyses were conducted to estimate the dietary preferences and feeding strategies of the monkeys, measured on the basis of how long (in %) they spent eating each food category e.g. fuits, leaves, wood, etc. For the statistical analysis, a non-parametric Mann-Whitney U test was done for each of the three species in order to compare if the time spent on the different food categories was different. The comparisons were done only for fruits and leaves, given that the other categories did not have enough observation for statistical analysis.

Dietary preferences for *A. hybridus* estimated from feeding bouts

For *A. hybridus* the dietary preferences (e.g. fruits, leaves, etc) are presented separately for the total time of the study (June 2008 –February 2009). For this species it was also possible to estimate the dietary preferences regarding some of the plant species, given that initially more observations were allocated on this species and data were collected with more training people regarding the flora of the area.

The percentage of feeding time upon each plant species was calculated with a frequency analysis. From this analysis, the most common species of which *A.*

hybridus is mainly feeding on were selected. The criterion was those individuals per species with ten or more observations (≥10), means for the analysis only the plant species registered with more than 10 observations were having into account. Having in mind the species which were visited more frequently by the monkeys, Chi^2 tests and the non-parametric Kruskall-Wallis tests were done, since it was necessary to compare two samples that were not normally distributed. The Chi^2 test was applied in order to estimate differences between the types of item consumed (fruits/leaves) per plant species. The Kruskall-Wallis test was used to estimate the mean time spent per feeding item.

Georeferencing of the trees

Each feeding tree was marked with flagging tape and a unique number was written in a metal tag in order to identify the tree. Whenever possible, botanical samples were collected in order to identify the trees with the help of the botanist of the project. The location of each tree was registered, each feeding tree in relation to the marked reference points in the forest or to the previously marked trees, in order to have a precise location of each feeding source.

Coordinates were calculated in EXEL in the Universal Transverse Mercator (UTM), and the mapping was done using GIS, ArcMap 9.2. To estimate if there was dietary overlap between the species, the resource trees for *A. hybridus* were mapped, since there were not enough reference points for the trees of the other two species, as explained before there were not enough observations on the feeding bouts for *C. albifrons* and *A. seniculus*. However, the trees identified as a feeding resource are distributed all along the forest, so the same feeding trees could be being employed for the three sympatric species of monkeys.

Seed dispersal by the primate community

Fecal samples

To compare the seed dispersal patterns of *A. hybridus*, *A. seniculus* and *C. albifrons,* we collected as many fecal samples as possible from our study groups. Fecal samples were collected from focal groups only; no fecal samples found in the field opportunistically were collected. However due to flooding periods it was not possible to collect a large enough quantity of fecal samples, especially for *A. seniculs* and *C. albfrons*. Given the unusual patterns of this study year, were the raining season was stronger, most of the time of the study period the forest was flooding, and many areas were inaccessible, the flooding was stronger late September up to early December.

We marked each fecal sample and record the species, group, individual (when possible) that defecated as well as the time and the location of the defecation. Each independent fecal sample was put in a separate plastic bag and taken to the station. To identify the plants dispersed by each primate species, each fecal sample was cleaned with a 1 mm mesh and all seeds were counted and identified. Given that some of the plants were already identified it was possible to classify seeds into species, others only as morphospecies. For those plants that have very small seeds (e.g. figs) seeds were estimated in three categories: X (20-50 seeds), XX (50-200 seeds) and XXX (200 or more seeds); and the lower number was used for the analyses. Nevertheless it was not possible to identify most of the seeds found in the fecal samples.

Seed dispersal patterns

To describe the temporal and spatial seed dispersal patterns of the primates, we recorded the exact position of the defecation, based on the references points in the trail system (both feeding trees and references trees). The coordinates were calculated and together with the feeding trees were introduced into ArcGis.

Two kinds of maps were generated. The first one included the spatial location of the seeds for which it was possible to identify their number and species, in order to measure the distance to the nearest mother tree and have an estimate of the seed dispersal patterns of the three monkey species. Not all the trees present were identified, so the distance was measured to the closest identified tree. Given that not all of the feeding trees used by *A. seniculus* were mapped, its dispersal distances were measured relative the trees used by *A. hybridus*, so it is probable that the dispersal distances for *A. seniculus* are overestimated.

Since few sets of seeds contained information about the kind of species dispersed by the monkeys, a second map was generated including the locations of all the fecal samples collected, in order to have a better estimate of the geographical distribution of the seeds dispersed by the monkey community. This was done considering home ranges, estimated with the kernel method (see below for an explanation of home range).

Primate habitat use and home range

To understand the way the primates are using the space partitioning or sharing the area in the forest, the home range was estimated in order to have an idea on how the space is the limited factor in the forest fragment, and link it with the different patterns found from the feeding behavior analysis.

Home range estimation

From each scan sample, for each primate taxa in the study area, we collected data every 15 minutes on the location of the target group. The coordinates were calculated and the data was used to estimate the home range of all recognized social groups using the Animal Movement extension for ArcGis. Home ranges were established for the two groups of *A. hybridus* and for the three identified groups of *A. seniculus*. For *C. albifrons*, it was not possible to establish the ranging, since the groups are not yet completely identified. The home range of the species was determined with three methods: the Minimum Convex Polygon, Kernel, for *A. hybridus,* additionally the home range was estimated as the Minimum Polygon.

Minimum Convex Polygon (MCP): This method calculates the home range size by drawing a convex polygon around the location points of an individual (Boyle *et al* 2008).

Kernel: Uses non parametric statistics to calculate the probability of find an individual in a particular location, by assign an area surrounding each point. The kernel was estimated as the fixed kernel (with the 95% of the data), and as the adapted kernel (with the 50% of the data), since the method tend to overestimate the range of the species (Boyle *et al* 2008).

Minimum Polygon: Given that the MCP overestimated the range of *A. hybridus* (because of the particular shape of the forest). This method was designed joining the periphery points for the registered locations for each group.

Habitat use estimation

In order to identify inter-specific competition in terms of dietary overlap and habitat use, the kernel method for the home range estimation of *A. hybridus* and *A. seniculus* was used as reference. For the habitat use, the ranging area of *A. hybridus* and *A. seniculus* was overlapping together with the sighting points of *C. albifrons*. For the dietary overlap, the feeding trees were plotted together with the home range of the mentioned species.

The intensity of habitat use was estimated for *A. hybriuds* SJ1 and SJ2 groups and for *C. albifrons*. Additionally for both groups of *A. hybridus,* the feeding trees were plotted to evaluate if there was a relation between the feeding tree and the intensity of habitat use. The area was divided into grids of 50 m x 50 m, where the animal sightings were plotted, the intensity of use of the area was classified into high, medium or low. These figures (18 A,B,C) were obtained from the research group.

Results

Activity budgets

Activity budgets are presented as the percentage of scans where a given activity was observed relative to the total number of scans recorded for a given primate species.

Scan sampling

Social activities were not frequent in any of the species studied (table 3). The species studied allocated their time in different ways (see statistics below). *A. hybridus* spent the major percentage of its time by travel followed by resting and feeding. *C. albifrons* allocated most of its time eating, but this was close to the percentage of time allocated to moving, whilst resting was almost negligible. In contrast to the two species above, *A. seniculus* spent most of the percentage of its time by resting, whereas feeding and movement were not as important (table 3).

Table 3. Percentages of the time spent on each behavioral category by the sympatric A. hybridus, A. seniculus and C. albifrons in a fragmented forest at San Juan de Carare, Colombia. Data are expressed as a percentage of the total number of scans where a particular activity was detected, and include adults, sub-adults, males, females, and an 'unidentified gender' category. N=total number of scans for the study period (June 2008 –February 2009).

	Activity budgets (%)					N
Species	Feeding	Social	Rest	Movement	Others	
A. hybridus	23,1	7,04	26,9	42,2	0,7	7 725
A. seniculus	7,0	1,8	80,5	10	0,6	5 711
C. albifrons	50,8	1,6	5,0	42,2	0,5	2 160

A. hybridus spent over 50 percent of its feeding time on fruits, followed by leaves, young leaves being consumed more often than mature ones. The main item on *A. seniculus'* diet, was leaves, and contrary than *A. hybridus,* mature leaves were consumed more often than young leaves, the second most frequent category was fruits. However it is important to bear in mind that *A. seniculus* spent only 7 percent of its time feeding. *C. albifrons* spent most of its feeding time foraging (feeding on different resources on the substrate, mainly insects) (table 4).

Table 4. Time spent on each feeding sub-category by the sympatric *A. hybridus, A. seniculus* and *C. albifrons* in a fragmented forest at San Juan del Carare, Colombia. Data are expressed as percentage of number of scans where a behavior in a given sub-category was detected, relative to the total number of scans recorded as 'feeding'. Data include adults, sub-adults, males, females and an 'unidentified gender' category. N=total number of scans for the feeding category and for each sub-category during the study period (June 2008 -February 2009). Bold numbers indicate items that were most frequently consumed.

		A. hybridus		*A. seniculus*		*C. albifrons*	
		N	%	N	%	N	%
	Feeding category	1781	100	399	100	1097	100
Subcategory	Flowers	6	0,3	3	0,8	0	0
	Foraging	0	0	0	0	757	**69,0**
	Fruits	971	**54,5**	*140*	**35,1**	312	**28,4**
	Mature leaves	137	**7,7**	154	**38,6**	10	0,9
	Young leaves	371	**20,8**	91	**22,8**	4	0,4
	Undetermined leaves	7	0,4	0	0	1	0,1
	Insects	0	0	0	0	5	5
	Wood	43	2,4	0	0	0	
	Other	232	13,0	10	2,5	0	0
	Seeds	10	0,6	0	0	0	0
	Out of sight	4	0,2	1	0,3	3	0,3

The three monkey species studied fed throughout the day (Fig. 11). *C. albifrons* and *A. hybridus* fed with a higher frequency than *A. seniculus*, and the three of them showed a higher feeding frequency around 4 hour clock pm, i.e. before the end of their daily activities. This figure is different from the percentage of the feeding time, but let us know the distribution of feeding along the day. From this figure it is possible to say that there are not differences on the resources segregation along the day, since the three species of monkeys fed at the same time.

The three monkey species allocated significantly different amounts of time to each of the main behaviors recorded ($\text{Chi}^2 = 2226{,}196$; Df=8; $p<0{,}0001$), e.g. resting vs. feeding. Furthermore, they also allocated different amounts of time to each of the feeding sub-categories ($\text{Chi}^2 = 899{,}060$; Df=8; $p<0{,}000$; $p=0{,}000$). The tendencies were same as previously explained, where *A. hybridus* is mainly eating fruits, *A. seniculus* is mainly in eating leaves and *C. albifrons* is mainly foraging (manipulation of the substract to get insects)

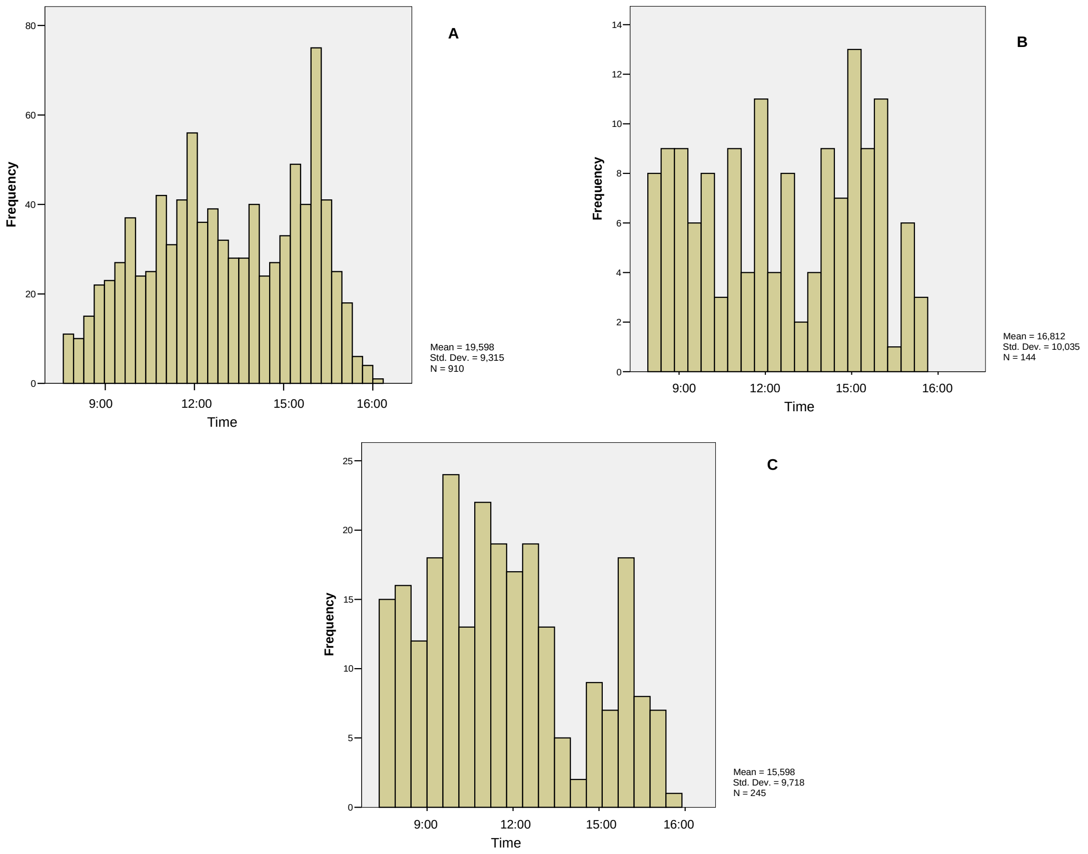

Figure 11. Frequency of the time distribution for the feeding categories along the day for the three monkey species from June 2008 to February 2009, the frequency was obtained from the scan sampling method. N=Number of observations.

Primate feeding behavior

A. hybridus dietary preferences estimated from feeding bout analysis

Results are presented both per month and per total observation time spent on each feeding source. *A. hybridus* was shown to eat mainly fruits, 53 percent of the total feeding time (Fig. 5). Nevertheless, there were two months (October 2008 and November 2008) when fruit consumption decreased, and a concomitant increase in the consumption of leaves was observed (Fig. 6). In December the percentage time invested in eating fruit increased again, although it did not return to June – September levels, and remained almost constant until February (Fig. 6). It is also worth noticing the strong increase in wood consumption in November, 37 percent vs. the 3 percent average for the whole study period (Fig. 5). Leaves, after fruit, were the second most important' food category for this species (Fig 5). There was an overall decrease in the time spent (per month) by *A. hybridus* consuming fruit, from around 60 percent at the beginning of the study to around 40% at the end (Fig. 6).

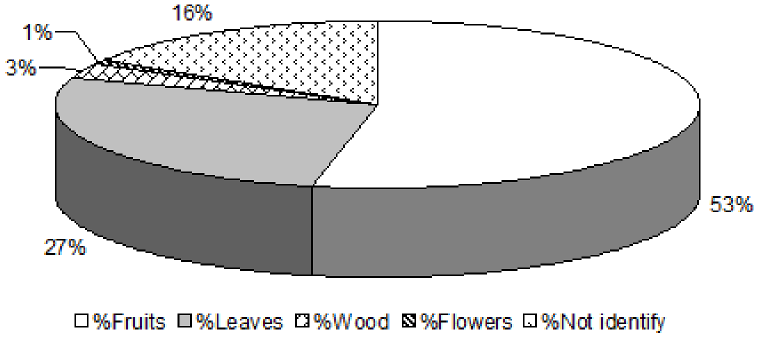

Figure 5. Total time from June to February (in %) spent on different feeding resources by A. hybridus . Seeds (0,5%), 20 minutes were also part of the diet. N=4231. N is indicating the total time expressed in minutes. In the pie chart, the numbers next to the percentage indicates the total feeding time (minutes) spent by the species on each feeding category.

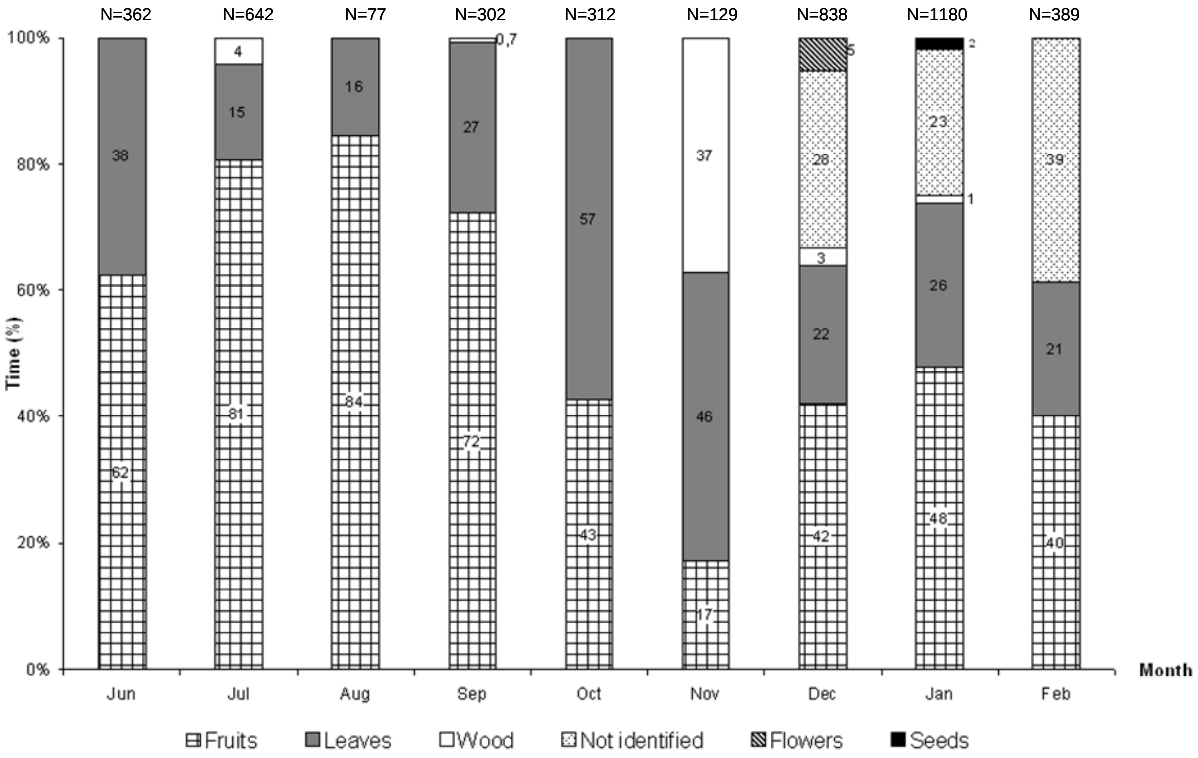

Figure 6. Total monthly time (in %) spent on different feeding resources by A. hybridus (from June 2008 to February 2009) at San Juan del Carare, Colombia. N= Total minutes spent eating on each month.

When time invested in eating fruits decreased, it was complemented with an increase in time invested eating other items. This is not in their 'normal' feeding behaviour when compared to findings from other studies (Di Fiore *et al* 2008) and read forward in discussion. It is important to highlight, in November there was low fruit consumption and the monkeys mainly fed on leaves and wood. In this month consumption of wood was important, representing 37 percent of the total feeding time. Nevertheless, except for November wood consumption was almost negligible. Similarly, November was a month with a low fruit consumption Strikingly, at the final of the study *A. hybridus* showed an increase in the percentage of time feeding on other items that were not identified, this was manipulation of the substrate, as is for example wood, but was not possible to identify what kind of food the monkeys were eating (Fig. 6).

Community dietary preferences determined from feeding bout analysis

Data for the feeding bouts of *A. seniculus* and *C. albifrons* was scant with low feeding records, only 604 observations minutes for *A. seniculus* and 413 observation minutes for *C. albifrons,* against 2407 observation minutes for *A. hybriuds*.

The diet of both *A. hybridus* and *C. albifrons* is mainly based on fruits and foraging is also important for *C. albifrons*. Both species complement their diet with leaves, (Fig. 7). In contrast. *A. seniculus* spent a high proportion of its time by eating leaves, followed by wood consumption. For *C. albifrons,* the percentage of time is fairly similarly allocated between fruits consumption and foraging (Fig 7).

Here is important to highlight that the no congruence on this results with those obtained from the activity budgets, for *A. seniculus* and *C. albifrons,* is due to the lack of data for this two species in regards with the feeding bouts, on the contrary, for *A. hybridus* there is congruence between the findings on the feeding bouts and the activity budgets. The bias stand in the total observation time, which is low for *A. seniculus* and *C. albifrons*, not only in total feeding time but also in the monthly feeding time (Figs. 7 & 8).

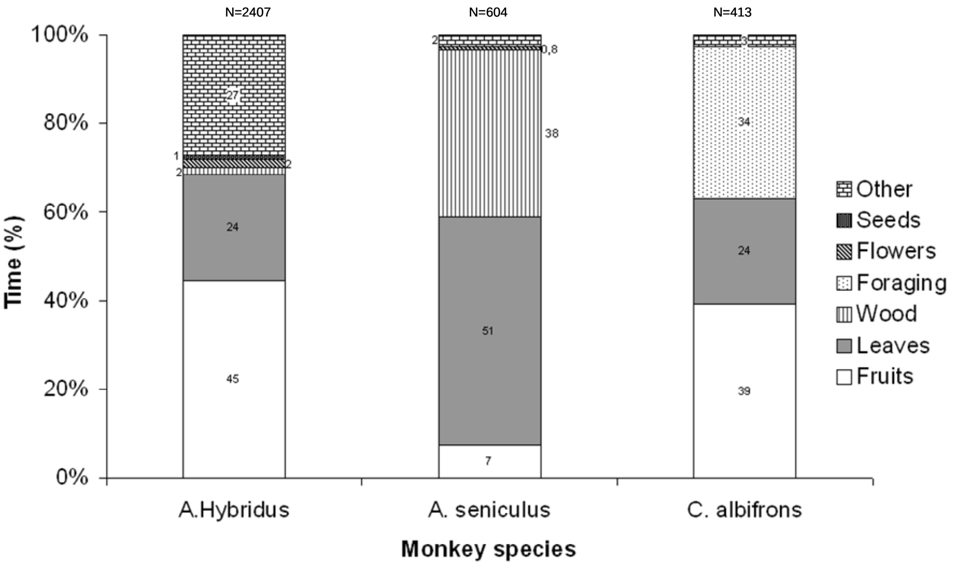

Figure 7. Total time (percentage) spent on the feeding resources by the three monkey species (December 2008-February 2009). N= Total minutes spent eating for the study period.

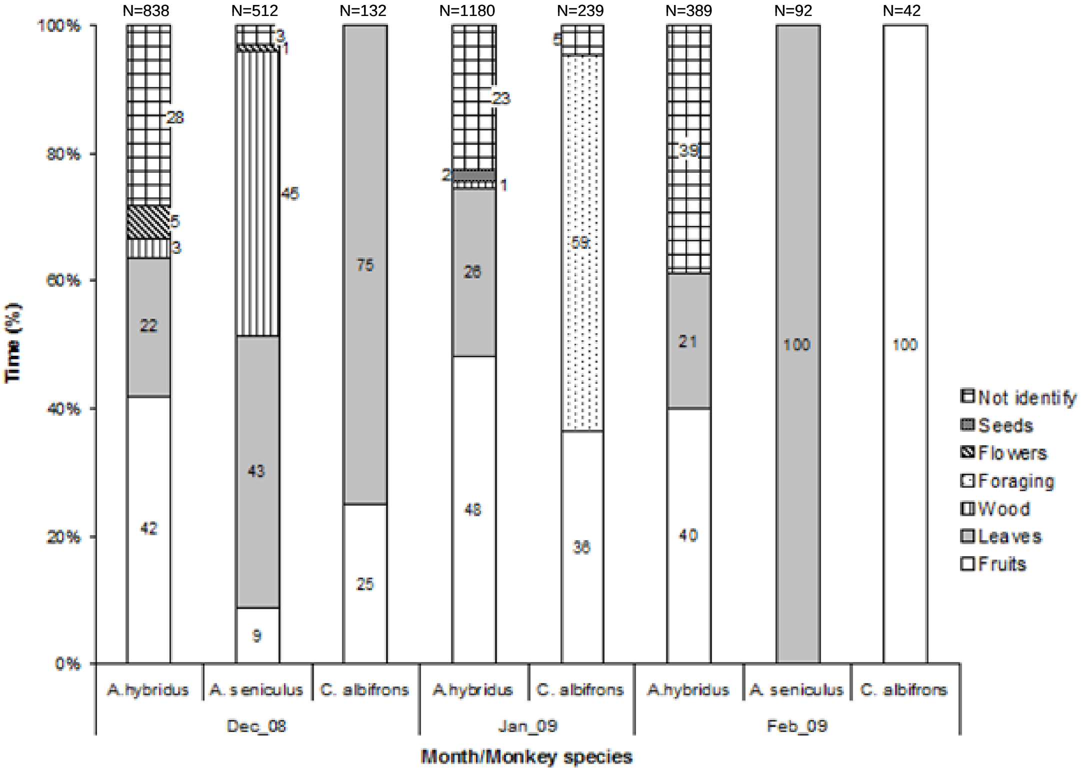

Figure 8. Time spent (in %) on each type of food by the three monkey species (from December to February). N= Total minutes monitored/month.

A. seniculus is a folivore species, but it is known to complement its diet with fruits (Whencke *et al* 2004), (Fig. 8). However, in February its diet was only based on leaves, and this was a month when *C. albifrons* was only consuming fruits (Fig. 8). It is remarkable that *A. seniculus* invested almost half of the percentage of the feeding time by eating wood in December (Fig. 8), despite its diet during the entire study period was based on mature leaves (Table 4; Fig. 9). December was also a month where *A. seniculus* spent the major percentage of their time eating young instead of mature leaves (Fig. 10).

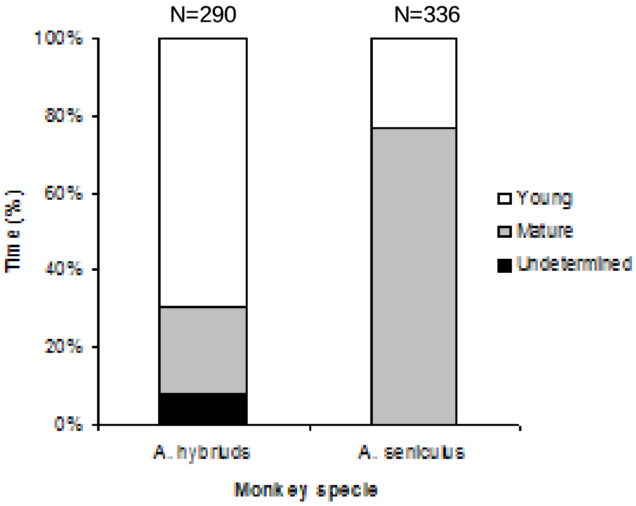

Figure 9. Maturity of the leaves in the diet of A. hybridus and A. seniculus. Comparissons from Dcember-February. N= Total minutes monitored for entire the study period.

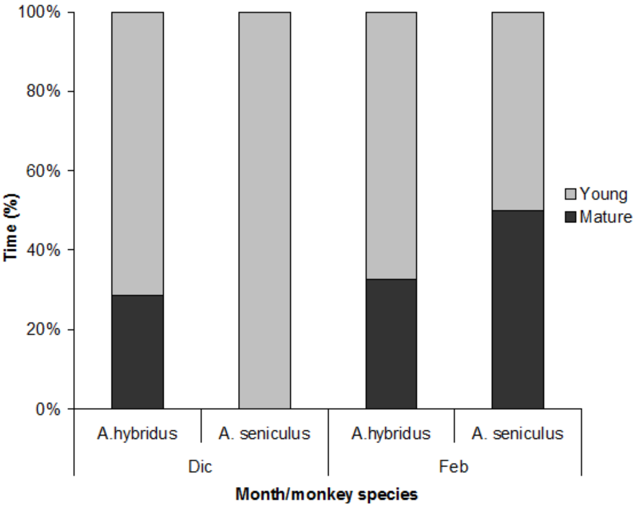

Figure 10. Maturity of the leaves in the diet of A. hybridus and A. seniculus, per month. Comparisons between December 2008 and February 2009.

A. hybridus spent significantly different amounts of time consuming leaves vs. fruits (Mann-Whitney U=23445,0, 2-tailed, P=0,0009, N=301 for fruits and N=189 for leaves). On the contrary, no differences were found for *A. seniculus* (Mann-Whitney U=76,0, 2-tailed P=0,4793, N= 6 for fruits and N=189 fir leaves) nor for *C, albifrons* (Mann-Whitney U=69,5, 2-tailed P=0,1908, N=22 for fruits and N=9 for leaves), maybe because of small sample sizes.

Dietary preferences for *A. hybridus* and tree species composition

From the feeding bout analysis it was possible to estimate (in some but not all cases) the tree species on which *A. hybridus* fed. A frequency analysis revealed that this species has a diverse diet (Fig. 12), feeding on over 18 plant species belonging to 12 different families (Table 5).

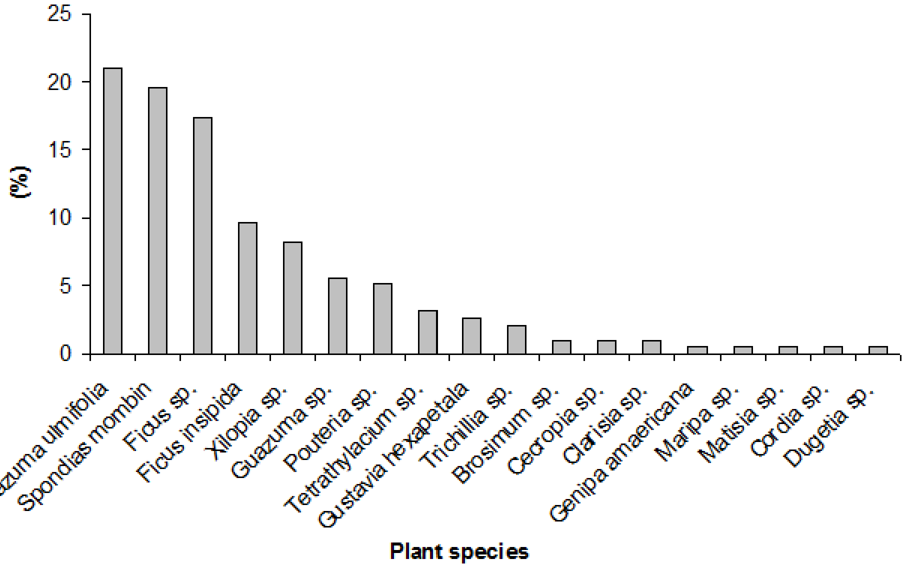

Figure 12. Frequencies of the plant species from which A. hybridus fed at San Juan del Carare, Colombia. Frequencies were based on the number of sightings per feeding plant from the June 2008-February 2009.

However, it is important to clarify that only a few plant species were identified in this study, therefore it is not possible to ascertain that the plants reported here are the principal or total components of *A. hybridus'* diet.

The species most frequently eaten were *Spondias mombin, Guazuma ulmifolia* and *Ficus* spp. (Fig. 12), *Ficus* spp. is the most common genus and Moraceae is one of the main families in the forest studied "Villanueva, B & Link A. pers. comm.". Fruits were the main plant part eaten, except for *Ficus* spp., where leaves were eaten most (Fig. 13).

Table 5. Feeding observations from the feeding bouts for A. hybridus in the different plant species from June 2008-February 2009, specifying the type of feeding resource consumed and the percentage of time spent on each one. N=number of observations of the monkey on each feeding tree.

Family	Species	Fruit	Leaves	%	N
Sterculiaceae	*Guazuma ulmifolia*	X		21	41
Anacardiaceae	*Spondias mombin*	X	X	19,5	38
Moraceae	*Ficus* sp.	X	X	*17,4*	34
Moraceae	*Ficus insipida*	X	X	9,7	10
Annonaceae	*Xylopia* sp.	X		8,2	16
Sterculiaceae	*Guazuma* sp.	X		5,6	11
Sapotaceae	*Pouteria* sp.	X		5,1	10
Flacourtiaceae	*Tetrathylacium* sp.	X		3,1	6
Lecythidaceae	*Gustavia hexapetala*	X		2,6	5
Meliaceae	*Trichillia* sp.	X		2,1	4
Moraceae	*Brosium* sp.	X	X	1	2
Urticaceae	*Cecropia* sp.	X		1	2
Moraceae	*Clarisia* sp.		X	1	2
Rubiaceae	*Genipa americana*	X		0,5	1
Convolvulaceae	*Maripa* sp.	X		0,5	1
Bombacaceae	*Matisia* sp.	X		0,5	1
Boraginaceae	*Cordia* sp.	X		0,5	1
Annonaceae	*Dugetia* sp	X		0,5	1

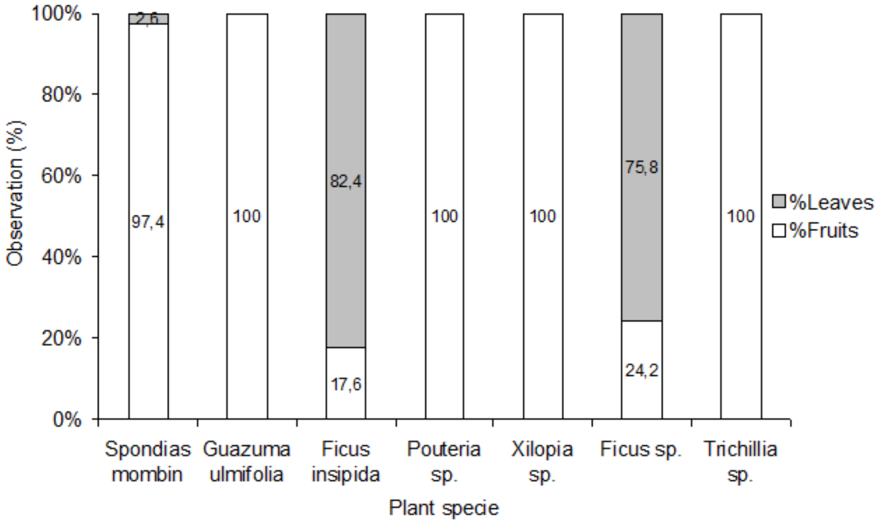

Figure 13. Number of observations (percentage) of each plant species per item: fruit or leaves consumed by A. hybridus (June 2008-February 2009) at San Juan del Carare, Colombia. The percentage is presented for the most common plant consumed (≥ 10 observations). N=166.

Comparing the kind of resource of the most common tree species eaten by *A*. hybridus, there are differences highly significant between the fruits vs leaves consumption (Chi^2= 7,29, DF=6. p<0,006). The Kruskal-Wallis test, also shows significant differences between the mean time spent per fruits between the different plant species (Chi^2=12,7092, Df=6; p<0,048). The results show that feeding bouts are longer for *Pouteria* sp, and *Guazuma ulmifolia.* In the same way the differences seems to be driven mostly for *Ficus,* since the monkeys are eating leaves form this plant species in a high proportion.

Seed dispersal by the primate community

Fecal samples

During the study time, it was possible to collect 47 fecal samples for A. hybridus, but only 16 fecal samples for A. seniculus and 13 fecal samples for C. albifrons. Table 6 shows the total number of seeds dispersed and the plant species dispersed by each of the monkey species on each collected sample.

Table 6. Number of seeds per fecal sample dispersed by A. hybridus, A. seniculus and C. albifrons at San Juan del Carare, Colombia. Most feces of the identified seeds presented here were collected in the period June-December 2008.

Family	Species	Number of seeds		
		A. hybridus	*A. seniculus*	*C. albifrons*
Moraceae	*Ficus sp*	5 900	0	0
Urticaceae	*Cecropia sp*	660	500	820
Fabaceae	*Inga sp*	81	0	0
Sterculiaceae	*Guazuma ulmifolia*	53	403	0
Meliaceae	*Trichillia sp*	47	0	0
Annonaceae	*Xylopia sp*	40	0	6
Anacardiaceae	*Spondias mombin*	26	0	0
Rubiaceae	*Genipa americana*	11	0	0
Sapotaceae	*Pouteria sp*	18	7	0
Rubiaceae	*Psychortia* sp.	0	3	31
Indeterminado		73	0	0
Total		6 909	913	857

Despite the small sample size, *A. hybridus* appear to act as an important seed disperser, since they are using not only a wide array of plant species, but also dispersing a high number of seeds per fecal sample.

A. seniculus and *C. albifrons* are dispersing similar amounts of seeds (913 vs 857 respectively), and dispersing *Psychotria* sp., which was not found in *A. hybriudus´* fecal samples.

Seed dispersal patterns

Table 7-9 present the plant species dispersed by the monkeys per fecal sample, and the distance to the closest identified con-specific tree.

Table 7. Dispersal distances by A. hybridus, at San Juan del Carare, Colombia. Distance stimation from the defecation place to the nearest con-specific tree. N=47. Each fecal sample was assigned a unique identification number, shown in Fig. 14, thus the dispersed plant species that have fecal samples with the same number means belong to the same fecal sample. Numbers were assigned at random, so that their order does not follow any pattern but. The mean of the dispersal distance is expressed with the standard deviation (sd).

Fecal sample	Dipersed plant species	Dispersal distance (m)
1	*Guazuma* sp.	305
34	*Trichillia* sp.	164
34	*Guazuma* sp.	149
34	*Ficus* sp.	85
46	*Ficus* sp.	175
46	*Trichillia* sp.	412
42	*Pouteria* sp.	566
43	*Pouteria* sp.	531
Xx	*Ficus* sp.	152
36	*Trichillia* sp.	144
36	*Ficus* sp.	74
30	*Trichillia* sp.	11
30	*Ficus* sp.	131
39	*Ficus* sp.	358
39	*Trichillia* sp.	126
9	*Ficus sp.*	530
7	*Ficus* sp.	207
6	*Ficus* sp.	207
2	*Inga sp.*	288
39	*Genipa* sp.	383
13	*Spondias mombin*	712
32	*Spondias mombin*	896
32	*Xylopia* sp.	321
32	*Genipa* sp.	86
37	*Spondias mombin*	1 024
44	*Xylopia* sp.	66
Mean±sd		443±430,13

For *A. hybridus* it was found that they are dispersing a wide array of *Ficus* seeds, however previously was found that form *Ficus* this monkeys are eating mainly leaves, the findings in the feces could be related with the idea that on single fig provides with a high number of seeds.

Table 8. Dispersal distances by A. seniculus. Form the defecation place to the nearest mother tree. N=16. Each fecal sample was assigned a unique identification number, shown in Fig. 14, thus the dispersed plant species that have fecal samples with the same number means belong to the same fecal sample. Numbers were assigned at random, so that their order does not follow any pattern but. The mean of the dispersal distance is expressed with the standard deviation (sd).

Fecal sample	Dispersed plant species	Dispersal distance (m)
1	*Cecropia* sp	513
1	*Guazuma* sp	55
2	*Cecropia* sp	619
2	*Guazuma* sp	77
3	*Pouteria* sp	125
4	*Cecropia* sp	499
5	*Cecropia* sp	222
5	*Guazuma* sp	303
Mean±sd		301±218,17

Table 9. Dispersal distances by C. albifrons. Form the defecation place to the nearest mother tree. N=13. Each fecal sample was assigned a unique identification number, shown in Fig. 14, thus the dispersed plant species that have fecal samples with the same number means belong to the same fecal sample. Numbers were assigned at random, so that their order does not follow any pattern but. The mean of the dispersal distance is expressed with the standard deviation (sd).

Fecal sample	Dispersed plant species	Dispersal distance (m)
1	*Cecropia* sp	44
1	*Inga* sp	54
2	*Cecropia* sp	73
3	*Cecropia* sp	95
4	*Cecropia* sp	161
5	*Psychotria*	704
6	*Xylopia*	439
8	*Psychotria* sp	125
7	*Cecropia* sp	22
9	*Psychotria* sp	1 295
10	*Cecropia* sp	110
Mean±sd		283±394,03

The distances from the defecation places to the nearest con-specific tree reflects that *A. hybridus* is dispersing seeds in average farther (443 m), followed by *A. seniculus* (303 m) and finally *C. albifrons* is the one dispersing it closer (283 m) (Table 7-9). It is remarkable that *A. hybridus* is not only dispersing a wide array and number of species, but also their ability to disperse its seeds far away from the con-specific tree. This species is moving seeds from 11 m to 1 887 m far from the con-specific tree, *A. seniculus* moved seeds from 55 m to 619 m and *C. albifrons* is dispersing seeds from 22 m to 1 295 m away from the closest con-specific tree (Tables 7-9). Longer distances for *A. hybridus* are related with the longer home ranges this species has in comparing with *A seniculus*.

However, for *A. seniculus* the dispersal distances can be overestimated, due to not all of its feeding tress were mapped, therefore the distances were measure with the feeding trees mapped for *A. hybriuds,* and some of this trees can be outside of the home range of the different groups of *A. seniculus*. For *A. hybridus,* Only 8 seeds were deposited less than 50 m far from the mother tree, 1 less than 50 m and also 1 less than 1 m. The spatial distribution of the fecal samples which contained identifiable seeds (Fig. 14A-C) indicate that the monkey species studied are moving seeds all around the forest.

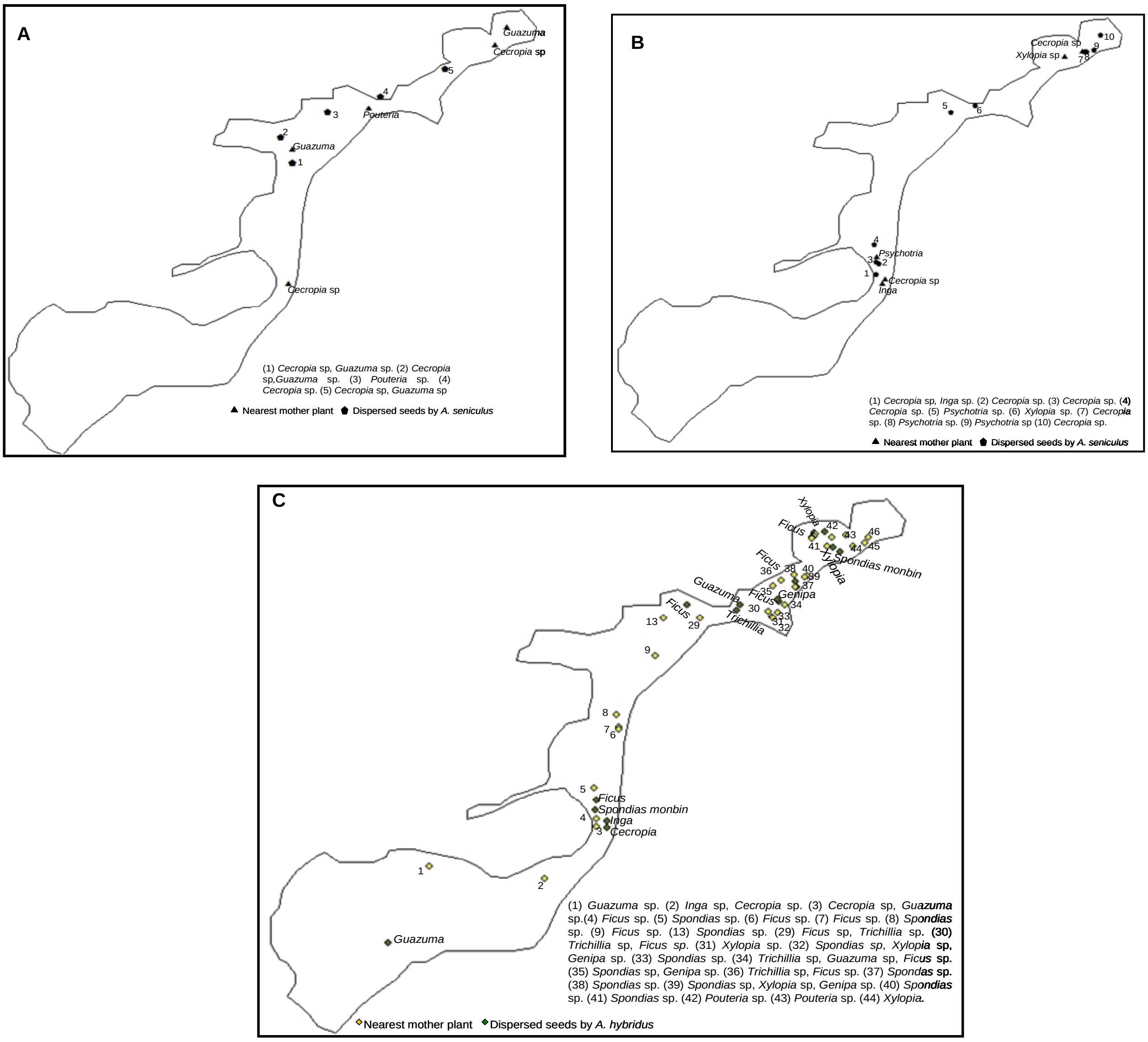

Figure 14. Map of San Juan del Carere showing seed dispersal patterns from the fecal samples of *A. seniculus* (A); *C. albifrons* (B); *A. hybridus* (C), in relation to the nearest feeding trees. The numbers in the map represents each independent fecal sample.

Primate habitat use and home range

Home range

For *A. hybridus,* the home range was estimated for the two groups that are living in the area (named SJ1 and SJ2), for *A. seniculus* the home range was estimated for three of the identified groups (named A, F and N), there is not accurate knowledge on how many groups of this species there are, but the population was estimated with the census (read next chapter). Each of the methods used yielded different home range estimates for both species (Table 10 and 11), therefore is important to compare methods.

Table 10. Home range estimation for A. hybrius (SJ1 and SJ2 groups) with the different methods. Home range is expressed in hectares.

Method	SJ1	SJ2
Minimum Convex Polygon	52.63	31,07
Kernel 50%	11,57	8,27
Kernel 95%	63,62	45,58
Minimum Polygon	18,95	21,68

The MCP home range estimate for *A. hybridus* is very close with tto that calculated with the kernel method (with 95 percent of the data) (Table 10). Home range overestimation for this species (SJ1 and SJ2 groups) is considerable with MCP (Fig 15A), the home range even extending beyond the forest boundaries and including the San Juan River. The MCP leads to overestimates because it does not distinguish between characteristics of the area (Boyle *et al.* 2008), as is a no regular shape of the studied forest, with an elongated and narrow shape.

Table 11. Home range estimation for A. seniculus (A, F, N groups) with the different methods. Home range is expressed in hectares.

Methods	A	F	N
Minimun Convex Plygon	0,26	1,85	1,52
Kernel 50%	1,18	1,43	1,56
Kernel 95%	4,29	4,63	5,69

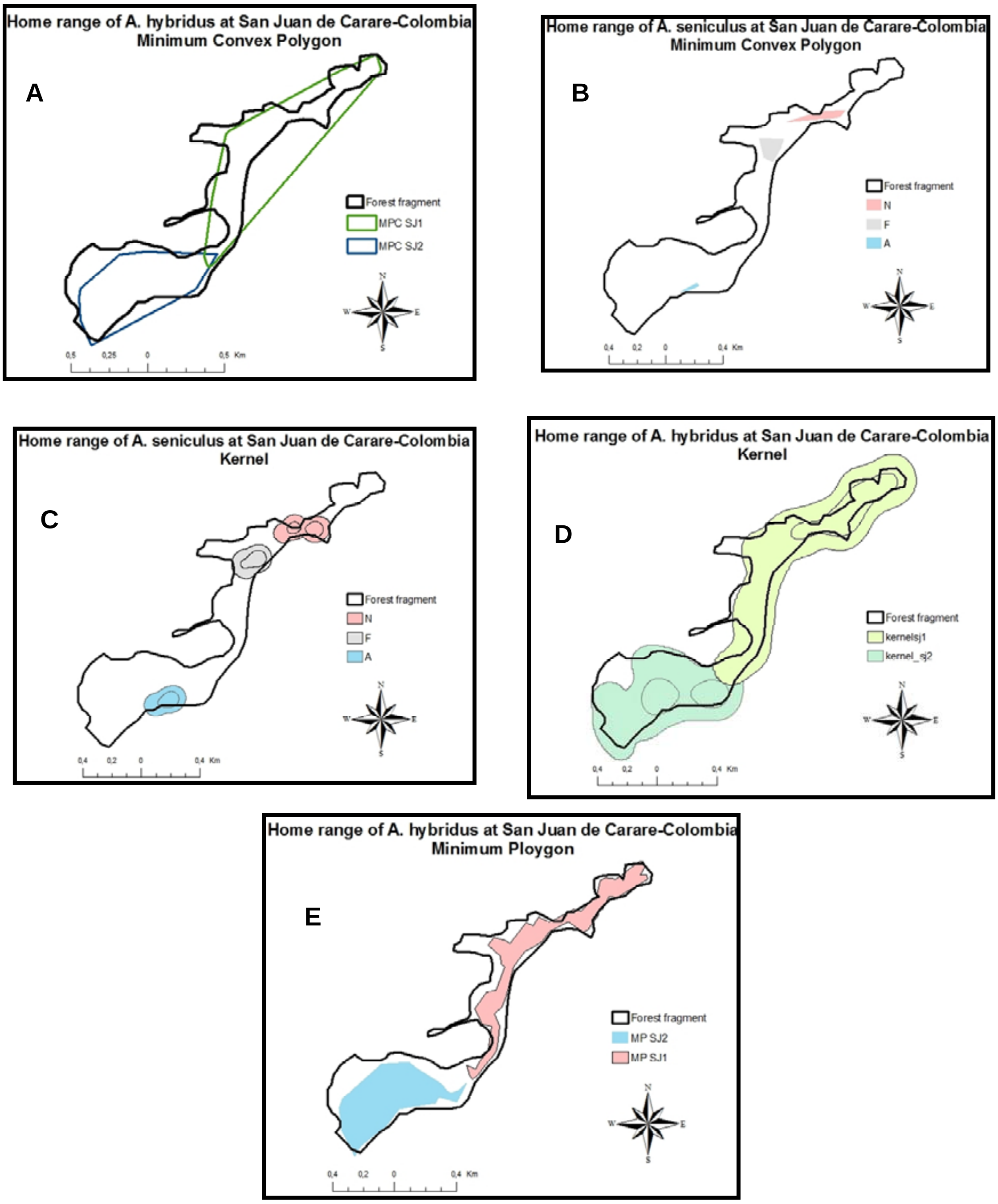

Figure 15. Home range for A. hybridus (Groups SJ1, and SJ2) and A. seniculus (Groups N, F, A) at the fragmented forest in San Juan Del Carare, Colombia, A and B. Estimated as the Minimum Convex Polygon for both species of monkeys. Notice the overestimation of the ranging for a. hybridus, which goes beyond the forest boundaries. C and D. Kernel

Comparing the Kernel (50% of data) with the Minimum Polygon for the SJ1 *A. hybridus* group, it is possible to say that this methods provide a more accurate estimation of the ranging (Table 10), however, Kernel is sensitive when data are not enough (Boyle *et al* 2008) (as with SJ2), and in this case the home range of the species is being underestimated, when using only the 50 percent of the data (Table 10), this is possible to say since the Kernel (95%) is giving an estimation higher than the MCP, in the same way whne comparing with the Minimun Polygon, kernel (50 percent) is lower. The Minimum Polygon method provides the most accurate home range estimate for SJ1 and SJ2, since this method joined the peripheric points of the location sightings of the individuals (Fig. 15E), therefore this method provides the most accurate estimation of the area the animals are using inside the forest. It is possible to observe that the MCP, draws an home range stimation that goes beyond the forest boundaries, different form the Minimum Polygon (Fig. 15A , E).

Home rage estimates for *A. seniculus* obtained with the MCP and Kernel (95 percent) methods provide a better estimate of the ranging of the species in the area (Table 11). Contrary to *A. hybridus*, the MCP method for *A. seniculus* is not overestimating its ranging, as is possible to observe from Fig. 15B. The Kernel method has the added advantage that it shows the major centers of use, by calculating the probability of find an individual in a particular location (Boyle *et al.* 2008), places where the animals are found more frequently within their home range. These major centers are illustrated with inner circles (Fig. 15C, D).

Habitat use

When plotting defecation places (dispersal places) (Fig. 16A, B) within home ranges estimated with the Kernel method, it is evident that that despite the fact that the monkeys are distributing the seeds all over the forest, seed dispersal is concentrated within areas of major intensity of habitat use (inner circles). This pattern is evident for *A. hybridus* (Fig. 16A). For *A. seniculus,* (Fig. 16B) on the contrary dispersal places are more common outside of their ranging area, but this can be because those three identified groups are not the only ones living in the area. Besides there are three groups identified, the followings of the animals are done with any group, even tough if are not those already identified. For *C. albifrons* the sample size for the fecal samples was low, they appear to move seeds all around the forest as well (Fig. 16C).

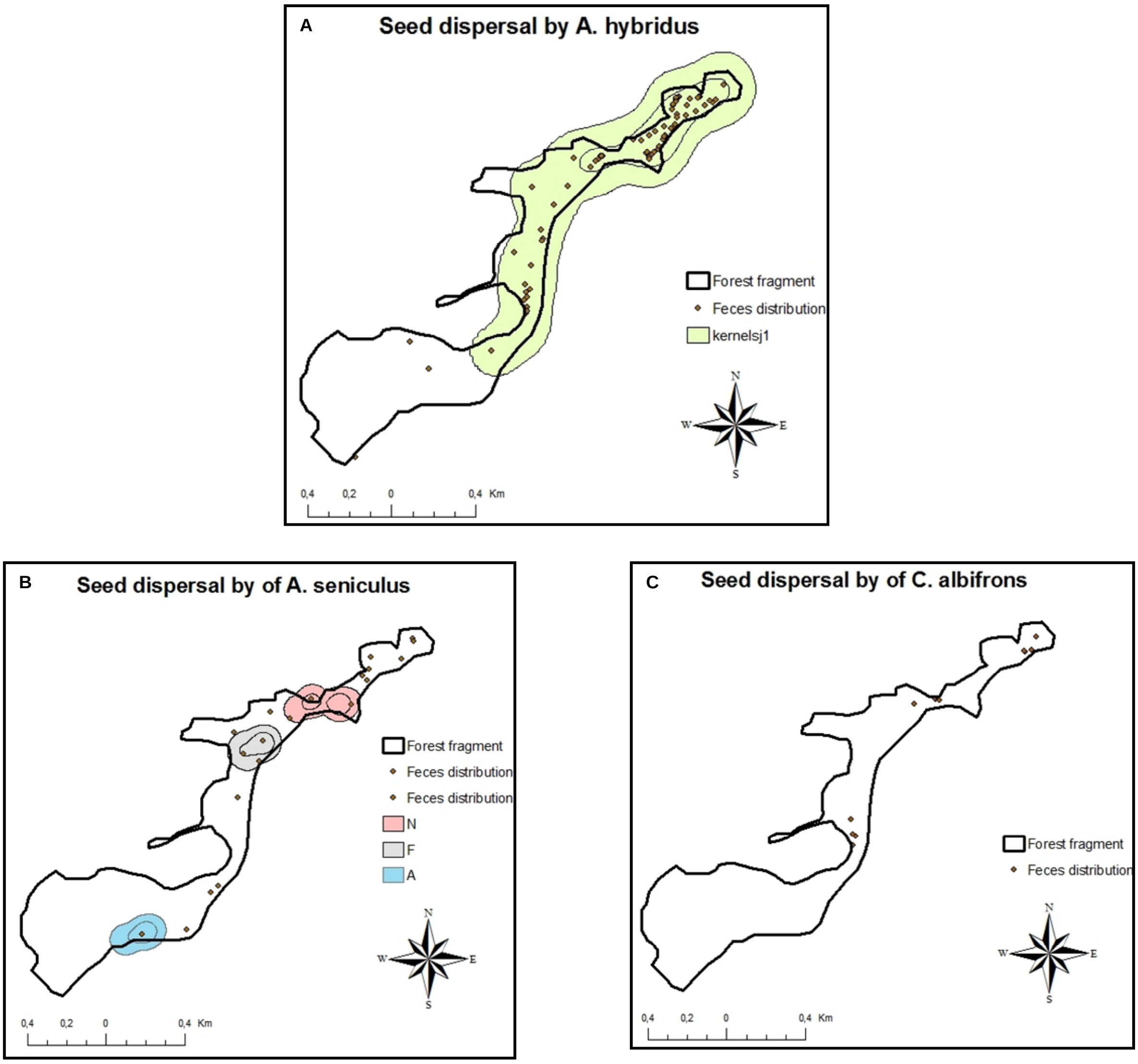

Figure 16. Spatial seed dispersal of the sympatric species A. hybridus, A. seniculus and C. albifrons at the fragmented forest in San Juan del Carare, Colombia. The former two species, with the home range with Kernel's method. A. Feces distribution of A. hybridus. B. feces distribution of A. seniculus. C. Feces distribution of C. albifrons.

Regarding with the habitat use, is possible to see how the species' ranges overlap (Fig. 17B) it. *A. seniculus* groups N and F overlap in area with *A. hybridus* group SJ1, but also group N's area of higher use is shared with that of SJ1 . Similarly, the area with higher use of group A is shared to some extent with that ofSJ2. Having in mind the location points were *C. albifrons* was sighted (Fig. 17A), is noteworthy that they seem to be distributed all along the forest sharing and overlapping areas with the other two species. In the same way, the areas of major use by *C. albifrons* (higher density of dots on the map) overlap with those of SJ1 and *A. seniculus* group N.

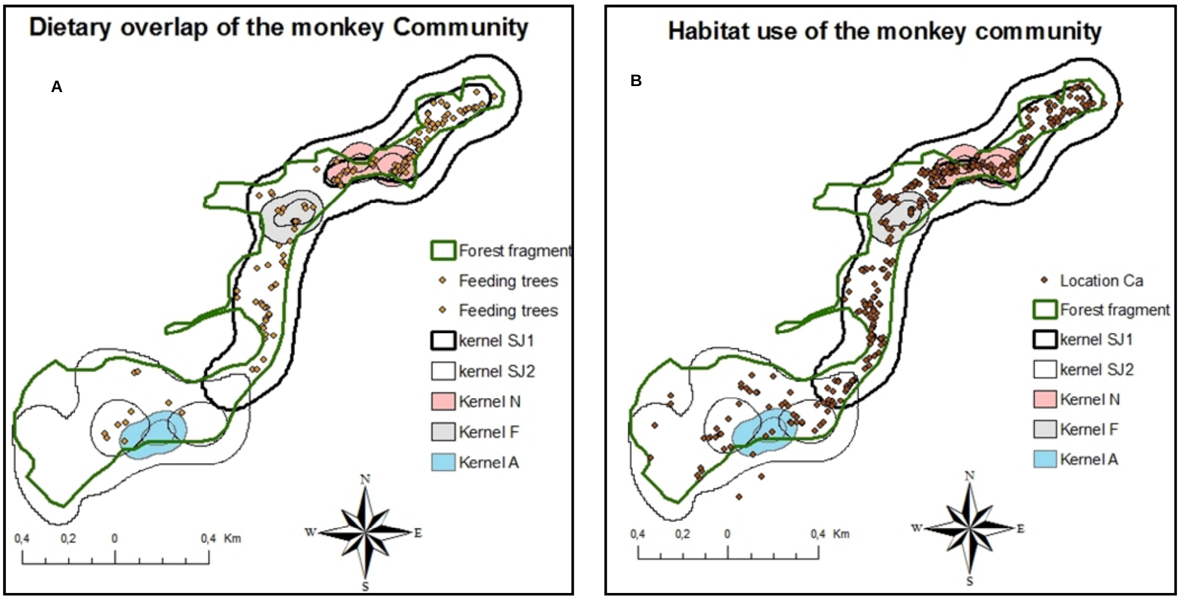

Figure 17. Habitat use and dietary overlap by the sympatric species at the fragmented forest at San Juan del Carare, Colombia, based on the Kernel method for home range estimation. A. Dietary overlap, location of the feeding trees regarding the home range of the species B. overlapping of habitat, for A. hybridus and A. seniculus and the location points were C. albiforns were observed.

When plotting the feeding trees relative to *A. hybridus* and *A. seniculus* home ranges (Fig. 17A), it is evident that the area which the three monkey species use intensively (indicated by a higher number of sightings registered) corresponds with a higher use of feeding trees; feeding trees are most frequently recorded in the area of major use by the three species of monkey. This area of higher use can definitely be a potential conflict area for them.

Regarding the study area's use intensity, the SJ1 group is using the forest from a medium to a high level (Fig. 18A), this imply the monkeys are using the habitat in an intense level, so the exploitation of the feeding resources is probably intense. The areas with higher intensity of use by the SJ2 group are close to those of *A. seniculus* (Fig. 17B), this is apparent despite the low quantity of data points. For both, *A. hybridus* and *A. seniculus* the places of higher habitat use are related to a higher frequency of feeding trees. In the same way, comparing the intensity of habitat use between *C. albifrons* and *A. hybridus* (Fig. 18C) is clear that their areas are overlapping completely. Although the areas of higher use intensity are slightly different in their extent, they are still being shared.

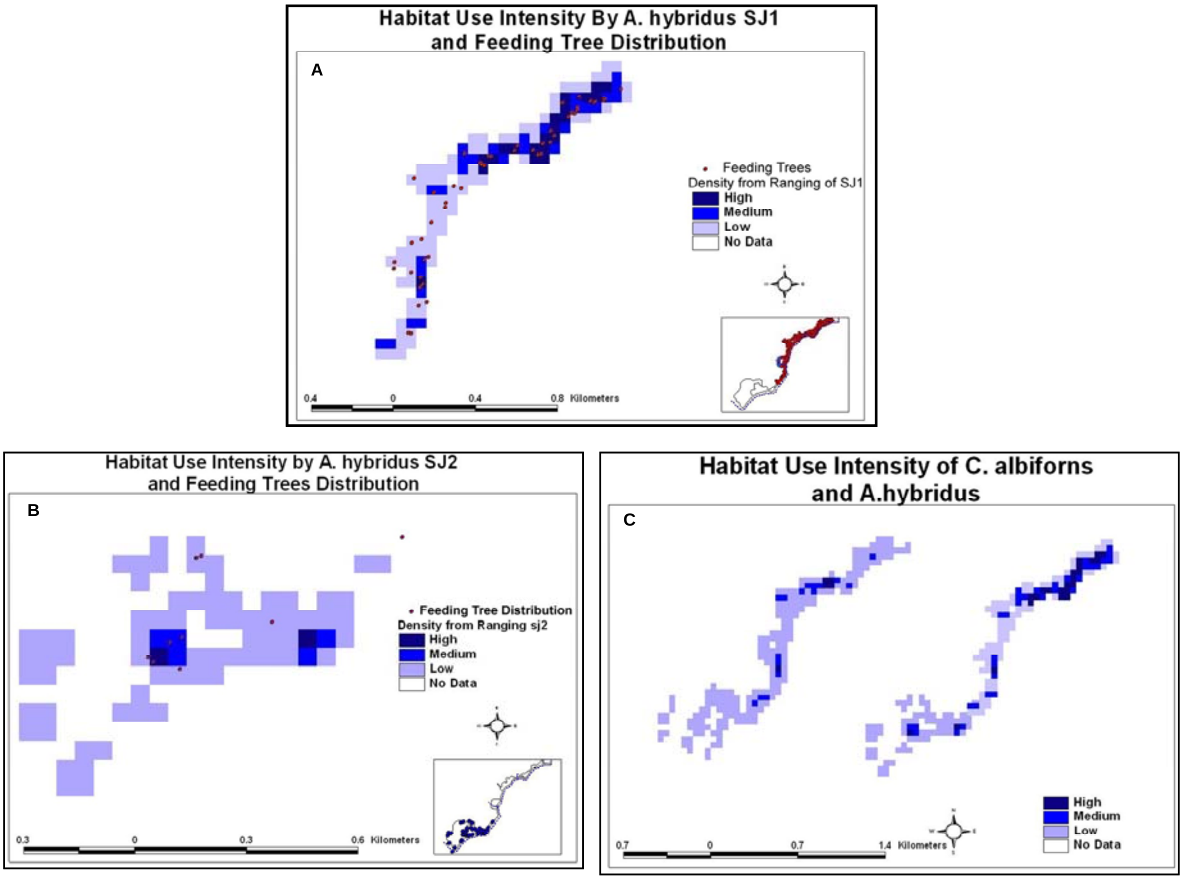

Figure 18. Intensity of habitat use, for A. hybridus groups SJ1, SJ2 and C. albifrons. A. Habitat Use intensity in relation with the feeding trees for SJ1 group. B. Habitat Use intensity in relation with the feeding trees for SJ2 group. C. Comparison of the habitat use intensity between A. hybridus and C. albifrons. Figure obtained form the research group.

These results imply that there is a dietary overlap between the sympatric *A. hybridus*, *A. seniculus* and *C. albifrons* at San Juan del Carare, where the three species may be facing scramble competition (see explanation in the following section), especially since they are exploiting the resources at the same times of the day. Displacements were occasionally observed from the feeding trees, especially it was possible to observe *C. abifrons* displaces *A. hybridus*, and that *A. hybridus* displaces *A. seniculus*. Moreover, when two groups of *A. seniculus* meet, vocalizations for territorial call were emitted; in fact they are doing it most of the day, as a secondary indicator of the stressful situation they are living in. However, more social studies are necessary to better understand the agonistic encounters between the species.

Discussion

At the present study, *A. hybridus* is playing the most important ecological role of the three studied species as a seed disperser in the studied forest fragment, given its preferences for comparatively broad variety of fruits, the quantity of seeds dispersed and the dispersal distances. However, we found that for *A. hybridus* the consumption of fruits is lower than what is reported in other studies (see references below).

Understanding the general foraging patterns of the three sympatric species, *A. hybridus*, *A. seniculus* and *C. albifrons*, allows us to understand the way they are partitioning their diets at this forest fragment, in order to survive in an small area (66 h.), with a population density of primates as high as 30 individuals per km^2 for *A. hybridus*, 124 individuals per km^2 for *C. albifrons,* and 68 individuals per km^2 for *A. seniculus* "De Luna, G & Link, A. unpubl." Primate's population densities at San Juan del Carare are high when comparing with other research areas of higher extension. Chapman *et al.* (1988), in a extensive forest in Costa Rica (10 800 h.), reported for *Alouatta palliata,* densities of 15, 2 individuals per km^2 and for C*ebus capucinus* densities of 17,38 individuals per km^2. In a 133 h. of forest in Colombian Andes, Posada *et al.* (2007) reported densities of 72,6 individuals per km^2. In Bolivia, in a 50 km^2 area, it was found densities of 14,1 individuals per km^2 for *Cebus apella.* and 32,1 individuals per km^2 for *Ateles paniscus* (Wallace *et al.* 1998)

.

The monkey community at San Juan del Carare seem to be facing feeding stress, where fruits can be limiting at least during part of the year thus making monkeys adapt their diets with feeding patterns not commonly reported (e.g high consumption of wood for *A. hibrudus* and *A. seniculus,* decreased in fruit consumption and increase in leaves consumptions for *A. hybridus).* Therefore, based on seven months of non-continuous observations it is possible to say that they are facing scramble competition, where in order to survive the community avoids competition by partitioning their diet (Cowlishaw & Dunbar 2000). By definition, scramble competition "occurs when the resource is limited but no single individual can monopolize it, so all competitors suffer equally from the effects of competition which is intensified with the number of competitors" (Cowlishaw & Dunbar 2000). Thus, there is a depletion of the limited resources and this result in a reduction of the foraging efficiency for all group members (Snaith & Chapman 2008).

It is important to mention that we cannot draw broad generalizations from our findings given that we only studied one fragment (at least two more replicates would be necessary to give more strength to the project, in order to compare the general patterns regarding with the feeding ecology in forest of different characteristics as is size, continuity with other forests and with different population densities of primates), for a period of only seven months, and the data gathering was not continuous. In the same way only one fragment of forest was evaluated, which does not make possible to compare our findings with the behavior of the species in the adjacent areas. However, those were the general observed patterns on the monkey community at San Juan de Carare and despite study constraints they seem to be different from other published studies (read references above), this is especially true for *A. hybridus.*

Activity budgets

The activity budgets of *A. seniculus* are mainly represented by resting, 80 percent of time spent in this activity, whilst feeding is almost negligible (7 percent) and movement is represented by 10 percent of time, it was also found that this species is moving more than the reports. Estrada (1999) who studied *A. palliate* and Andressen (1999) who studied *A. seniculus,* found that those species spent 3 percent of their total time on moving. *A. seniculus* at San Juan, similar as the literature reports, the species is in movement a bit more than twice the percent of time than the other authors have found. Regarding with the feeding and resting behavior, Estrada *et al.* (1999) found that *A. palliata* in a fragmented forest rested 80% of the time, but spent 17% of their time eating, Andresen (1999) in a continues forest, found that *A. seniculus* rested 63 percent of their time and ate for 18 percent. Thus, it is feasible that *A. senicuus* at San Juan del Carare not only is moving in a higher proportion of activity time, but also the proportion of time spent on feeding is lower, besides consistent with those authors the species at San Juan has resting as the main behavior, but this obey to the folivorous diet of the species, with low metabolic rates and home ranges (Andressen 1999)

Activity budgets for *A. hybridus* at San Juan del Carere indicated that this species mainly is moving, with a 42 percent of time spent in this activity, this activity is followed by resting and feeding, with fairly similar percent of time (27 percent and 23 percent respectively). Our findings are congruent with a study conducted by the same research group for *A. hybridus* at Las Quinchas, Colombia (Guerrero & Link 2007), which is also a fragmented forest, but has connectivity with another forest fragments. Guerrero & Link (2007) found that the species spent most of the percent of time moving (39 percent Quinchas), followed by resting (31 percent of their time) and lastly, feeding (23 percent of their time). The consistence between the two studies relays in the fact that the percent of time that the individuals of *A. hybridus* spent on each activity was slightly similar. Thus, at San Juan the monkeys spent a bit more of the total percent of their time in moving and a bit less in resting, than in Las Quinchas.

Three recent studies, conducted on extensive areas of forest, report that most of the time *Ateles* spp is found resting, followed by feeding and lastly movement. Andresen (1999) reported that *Ateles paniscus* in the Peruvian Amazon spent 31 percent of time resting and 22 percent of time in both: feeding activities and moving activities. Similarly Wallace (2004) found that *Ateles chameck,* in the Bolivian Amazon had resting as the first activity, followed by feeding and movement. Suarez (2006) in Ecuadorian Amazon forest found a similar time allocation for *Ateles belzebuth*. Comparing with these findings, the behavior of *A. hybridus* in San Juan del Carare thus differs from the general patterns of *Ateles* spp. in other areas of continues forests, as in those cases.

The no congruence of our results with the previous findings could be explained because the monkey community at San Juan could be experiencing a scramble competition. With scramble competition the groups obtain less food from feeding patches, so they must travel farther to get enough resources (Snaith & Chapman 2008), the food limitations at San Juan could be the reason why the species needs to search for food continuously, thus, the monkeys are spending higher percentage of time on movement than other studies have reported. The possible competition between the studied primates can also be explained because there does not seem to be resource segregation (i.e. daytime feeding partitioning) between the three monkey species at San Juan. The monkeys are actually exploiting resources at the same time of the day, with slight variations.

Feeding bouts

At San Juan, *A. hybridus* spent the major percent of the feeding time eating fruits. *A. seniculus*, was observed spending the major percent of the feeding time eating leaves, and *C. albifrons* spent the major percent of the feeding time feeding upon fruits and distributed feeding time in roughly equal proportions between fruits, leaves and foraging (mostly for insects). The feeding strategies and diet observed for the tree monkey species studied here are consistent with what different authors have described for species of the same genus elsewhere (see references below).

A. hybridus dietary preferences estimated from feeding bouts

At San Juan, *A. hybridus* spent 53 percent of their total feeding time by eating fruits. For *Ateles* spp, authors have reported larger percentages for the total time spent feeding on fruits (Dew 2001; Pozo 2004; Suarez 2006). Guerrero & Link (2007) found that *A. hybridus* spent as much as 94 % of its time feeding on fruits. For *A. belzebuth* in Brasil, Nunes (1998) found that fruits constitute 83% of the total time. Similarly, for the same species, three different studies carried out in Ecuador by Suarez (2006), Pozo (2004), and Dew (2001) revealed that the diet of this primate is composed by 78 percent, 70 percent and 87 percent of fruits respectively. Nevertheless, Di Fiore *et al.* (2008) states that generally in the Neotropics the genus *Ateles* spends between 55 percent to more than 90 percent of their annual feeding time by eating fruits. Our findings suggest that *A. Hybridus* in San Juan is not only at the lowest fruit consumption limit of what is generally reported for the genus, but also that comparing with other authors the species fed on fruits on a less percent of time. It is remarkable the small percentage of feeding time that*A. hybridus* is spending on eating fruits.

Leaves was the second item of preference in the diet of *A. hybridus* at San Juan, the monkeys spent 27 percent of their time in feeding in this category of food. It is known that *Ateles* spp. complement their diet with the consumption of leaves, this item is the second most important in the genus' diet, leaves represent from 7 percent to 20 percent of their feeding time (Di Fiore *et al.* 2008). Guerrero & Link (2007) found that leaves represent 6 percent of the total diet of *A. hybriudus.* Suarez (2006) reports that leaf consumption, represent 8 percent of the diet, is the third most important category, wood the second. From the our analysis, it was found not only that *A. hybridus* spent 7 percent more than the "upper limit reported" reported by Di Fiore *et al* (2008), but also that at San Juan this species are eating leaves in higher proportion of time than other species of the same genus.

From this research also was possible to analyse that there is a seasonal variation in leaf consumption, from low levels in July (15 percent) up to 57 percent in October, the low consumption of leaves in July is related with a high consumption of fruits (81 percent of time), and the high consumption of leaves in Octuber is related with low consumption of fruits (42 percent of time), November was also a month characterized by low consumption of fruits (17 percent of time), but the rest of the feeding time was not only complemented by leaves (46 percent), but with wood (37 percent) instead.

Pozo (2004) also reported a big monthly variation in leaf consumption, from 3 percent in January to 38 percent in August. In Tinigua National Park, Colombia, *A. belzebeth,* doubles the consumption of leaves and flowers during the end of the rainy season, which is a period of fruit scarcity (Link, Unpublished data in Di Fiori. *et al.* 2008). In the dry season, fleshy fruits again became the dominant constituent in *Ateles'* diet (Wallace 2005). Similarly, Stevenson *et al.* (1998) working in a tropical forest in La Macarena, Colombia (with similar seasonal rainfall than in our research area), found that there are two peaks of fruit production, one at the beginning of the rainy season (March-May) and another during the dry season (December-February), with fruit scarcity at the end of the rainy season (September-November). Stevensson & Ahumada (2000), found changes in activity budgets and diet, when studying the dietary overlap of four other sympatric species at La Macarena in Colombia, those changes were related with higher resting time, in periods of fruits scarcity.

It is difficult to draw general conclusions based on our data, since the study only lasted seven months, and there are not data regarding with phenological studies of the plants in the present study. Nevertheless we can say that the lower consumption of fruits by *A. hybridus* found here can not be attributed only to a seasonal effect, related with fruit scarcity as found by Stevenson *et al.* (1998), given that the rainy season had finished from mid December, and the consumption of fruits by the species did not increase. Similarly, it would be expected that the feeding behavior of the monkeys would be similar in the January-February dry season relative to the June-August dry season, however in January and February the percentage of time invested on fruit consumption was much lower. But again, the limitations of our data does not allow us to generalize these behaviors as annual patterns of the species studied

There is a lack of phenological data on fruit availability throughout the year for our study site. However, it is known that in rainforests trees can fruit all year round (Suarez 2006), although in different quantities and in different periods of the year. For example, Stevenson *et al.* (1998) found that in periods of the year characterized by general fruit scarcity, *Ficus* trees or palms (*Oenocarpus bataua*) can reach peaks of fruit production, and this plants provides fruits resources when the other plant species are not fructifying. The most important genera consumed by *Ateles* species, i.e. *Ficus, Brosimum, Inga, Cecropia, Pouteria, Protium* and *Virola*, do not fruit synchronously throughout the year, therefore they are found as main constituent on the diet of the genus in different places (Di Fiore *et al.* 2008). As a result, during periods of fruit scarcity when primate populations experience "nutritional bottlenecks", they rely on this type of plants which are considered keystone food resources and very important in the Neo-tropics, especially *Cecropia* and *Ficus* (Cowlishaw & Dumbar 2000; Di Fiore *et al.* 2008). At San Juan, Moraceae is one of the most important families "Villanueva, B & Link A. pers. comm.", but still probably the fruit supply is not enough for all the community, since the fruit consumption by the species remained low. The most frequently consumed plant by *A. hybridus* in San Juan del Carare is *Ficus* sp leaves. *Ateles* spp, is known to feed on the leaves from large canopy trees, principally from the families Moraceae and Bombacaceae (Di Fire *et al.* 2008). Despite a low total feeding on *Ficus* sp. fruit, seeds are abundant in each fig fruit.

Wood was highly consumed in November, a month of low fruit consumption, this month also corresponds to the rainy season and therefore fruit scarcity. The consumption of wood in November can be explained by the fact that it was a rainy period, with low productions of fruits and young leaves. *A. hybridus* at San Juan del Carare showed a preference to consume young over old leaves, and these findings are congruent with Dew (2001). Wood is not normally an important constituent of the diet of the genus (Suarez 2006). In fact, other studies do not even report wood as part of the diet of *Ateles* spp. Suarez (2006) however, found that decayed wood was the second most important item consumed by *A. belzebuth* in Ecuador, and also established that this is not a common item consumed by *Ateles* species. The wood consumption of *A. hybridus* at San Juan, can be explained given the probably low productivity of young leaves in this month, and since old leaves may not supply enough nutrients, the monkeys preferred to eat wood, probably mostly to fill their stomachs. Guerrero & Link (2007) also found that November was a month of lower fruit consumption for *A. hybridus*, but it supplemented its diet with leaves not wood. As opposed to the feeding behavior shown by *A. hybridus* in San Juan del Carare, the study carried out by Guerrero & Link (2007) does not show large monthly variation in the type of food consumed, and the diet of the monkeys at Las Quinchas was not as diverse as in this study.

Dietary preferences for the whole monkey community determined from feeding bouts

Despite the low feeding records for *A. seniculus* and *C. albifrons* (as explained in the methods and results sections), results indicated that *C. albifrons* are spending a third of their total feeding time eating fruits (39%), but with a monthly variation, were there is not a remarkable preference by any alimentary item. Thus on December the species fed mainly on leaves, on January the species mainly was feeding on insects (foraging feeding behavior) and on February *C. albifrons* consumed only fruits.

For *C. albifrons,* at the present study was found that the species spent fairly similar percent of time by eating fruits and foraging (39 percent vs 34 percent of time). Similarly, it is also important to highlight the findings on January, since this month is characterized by dry season, were supposedly fruits are in peak production, and therefore there should not be scarcity of the resource, however the species was mainly in foraging. *Cebus* species compensates for the scarcity of fruit by increasing total feeding and foraging times (Wehncke & Dominguez 2007), as was observed by this species at San Juan.

Similarly to *Aluatta* spp*., Cebus* species is considered as a non-restrictive frugivorous, and is mainly complementing its diet with arthropods (Stevenson *et al.* 2000; Wehncke & Dominguez 2007). Whencke *et al* (2003) reported that in Panamá, *C. capuchinus* spent 53% on fruit consumption, which is slightly similar with our findings. *C. capucinus* can spend between 70-90 percent of time eating fruits (Wehncke & Dominguez 2007), while other studies have reported a higher time looking for insects than eating fruits (Terborgh 1983, in Wehncke & Dominguez 2007). The ability of *Cebus* to switch on its diet from month to month was also reported by Chapman (1987). It has been found that they mainly do this in periods when other resources are scarce (Chapman 1988).

Consistent with those authors, our findings show that *C. albifrons*, varied preferences for different items during tree months of comparisons.

For *A. seniculus* it was found that two thirds of its diet is based on leaves (51 percent of feeding time investing on leaf consumption), and one third is complemented by eating fruits (7 percent). Andresen (1999) reported that this species ate leaves 56 percent of its time and fruits the remaining 44 percent. Julliot & Sabatier (1993), found the same species in French Guiana, spent 54 percent of their time eating leaves, and 22 percent eating fruits. Comparing with this authors, *A. seniculus* at San Juan del Carare, is spending a lower proportion of their feeding time eating fruits, despite the leaves consumption is fairly similar.

Allouata spp can have a highly frugivorous diet when there is low fruit production (Stevenson *et al.* 2002), Estrada *et al.* (1999), found that *A. palliata* spent five months of the year eating mainly fruits. However, from our results, *A. seniculus* in February feed only on leaves. This could supports that *A. seniculus* subsists on mainly folivorous diet in periods of fruit scarcity (Andresen 1999), however is important to have in mind that the sample size was not high on this month, with only 92 minutes of feeding records.

The current analysis indicated that contrary with *A. hybridus* which was mainly feeding on young leaves, *A. seniculus* is mainly eating mature leaves. Estrada *et al.* (1999), who studied the feeding behavior of *A. palliata* for one year in a small fragment in México, found that the species prefer young leaves over the mature ones. Thus, it is possible to say that *A. seniculus* at San Juan is experiencing a shift regarding leaf consumption.

Since mature leaves does not seem to be a prefer item by monkeys, probably *A. seniculus* at San Juan is only spending 7 percent of their time on feeding because the mature leaves may not be nutritive enough for this monkeys.

Comparing the leaf consumption between *A. hybridus* and *A. seniculus,* in December the consumption of young leaves was higher for *A. seniculus*, since both species were consuming this item, probably the resource was not enough for both of them and therefore A. *seniculus* shift its diet by increasing wood consumption, which represent the major percent of their feeding time (45 percent) on that month.

Similarly than with *Ateles* spp., wood is not a main item for *Aloutta* genus neither. Comparing with other studies, Julliot & Sabatier (1993) found that bark represented only the 0,4 percent of the diet of *A. seniculus* in a 19 months-observations period. From this it is possible to say that *A. seniculus* is also experiencing a shift o their diet, suggesting that this species may experience lack of nutrients, or feeding stress, since its diet feeding behavior is quite different from what is normally known for the species.

Dietary preferences of *A. hybridus* and tree species composition

The analysis done for the tree species composition in the diet of *A. hybridus,* does not show the real preferences on the diet of the species, the bias of this result is based not only in the lack of knowledge at the moment of register the tree species consumed by the monkeys but also that some of the tree species are still in identification process. However, was possible to identify in a broad sense some of the species of trees which *A. hybridus* feeds on.

In the present study it was found that *A. hybridus* feeds on 18 plant species, with preference for *Spondias monbin, Guazuma ulmifolia, Ficus insipida, Pouteria* sp., and *Xylopia* sp.

Several authors have reported on the diverse diet of the genus *Ateles*. For *A. belzebuth,* Link & Di Fiore (2006) found they are eating 152 fruiting species, and Suarez (2006) reported as many as 238 different plant species for fruits and additional five plant species for leaves grouped in 96 genera. Dew (2001) reported 44 different genera with 73 different species.

Di Fiore *et al.* (2008) from a cross-site comparisons of the diet of *Ateles* species around all the Neotropical forests, found that even though their diets are diverse only few plant taxa typically make up the bulk of their diet, these plant taxa are abundant in all of the sites. Their findings show that *Ficus, Brosium, Spondias, Inga, Cecropia, Pouteria, Protium* and *Virola* were the most common genera consumed. These are considered keystone resources and are regarded as crucial for the survival of primates in periods of fruits scarcity (Cowlishaw & Dumbar 2000; Wallace 2005). All the genera of plants mentioned above are abundant and fructify throughout the year (Di Fiore *et al.* 2008; Wallace 2005)

From this study *A. hybridus* consumed *Spondias, Ficus,* and *Pouteria* in a high proportion. This is important to highlight since *Ficus* is one of the most abundant species in this forest “Villanueva, B & Link A. pers. comm.”, as well as in the whole of the neo-tropics, they are a key resource since they do not fruit at the same time of the year, allowing animals to find at least some *Ficus* trees fruiting at any given time in the same forest (Dumbar 1988 in Cowlishaw & Dumbar 2000). In the same way we found *Cecropia* seeds in the feces of not only *A. hybridus,* but also of *A. seniculus* and *C. albifrons* as an indicator that the three species of monkeys were feeding on that plant as well.

Seed dispersal

With regards to dispersal patterns between the three species of monkeys we can only describe trends, given that data were scarce in terms of plant species dispersed, since not all of the seeds which were find on the fecal samples were identified, and dispersal distances, since not all of the feeding trees were mapped, at least for *A. seniculus*. Therefore the results presented here can not be estimated as the actual dispersal ability of the monkeys.

Regarding with the seeds-species found in the fecal samples, in our study, *A. hybridus* dispersed seeds form eight plant species; those plants present seeds from a wide array of size, from small sized-seeds like *Ficus,* to large-seeded size like *Pouteria.* Seed size results are comparable to the findings by Link & Di Fiore (2006) for *A. belzebuth* in Ecuador, which feeds on a wide variety of fruiting trees, dispersing seeds that range from *Ficus* sp., with seeds that are ≤ 1 mm up to seeds of 39 mm as those of *Pouteria.*

In our study, for *C. albifrons,* it was possible to find seeds from four plant species on the fecal samples, from those species, *Cecropia* was the most dominant. While studying *C. capucinus,* Wehncke *et al* (2003) found that in 90 percent of the cases they disperse *Cecropia* and *Ficus.* At San Juan del Carare, *C. albifrons* is showing same preferences in terms of plant species consumption.

For *A. seniculus,* it was possible to find this species dispersed the seeds from three different plant species; this seeds vary in size, from small as *Cecropia* up to bigger size like *Pouteria.* Estrada *et al.* (1999) found *A. palliata* disperse mainly *Ficus* and *Cecropia.* Andresen (2002) in an study conducted in Brazilian Amazon, found that *A. seniculus* fed mainly on plant species belonging to Sapotaceae, Moracea and Leguminoseae families. Our findings are consistent with both studies, since the fecal samples of *A. seniculus* mainly contained *Cecropia*, but also *Pouteria* was found. *Aloutta* has the ability to swallow big seeds, Andresen (2002) found in the feces form *A. seniculus,* seeds ranging from <3mm up to 32 mm, belonging to Moraceae and Sapotaceae respectively. At San Juan, it was proved the ability of this monkey species to disperse large seeded-trees, as *Pouteria.*

Comparing the seed dispersal of the three monkey species, it is possible to say that *A. hybridus* dispersed twice plant species than *A. seniculus* and *C. albifrons* at San Juan del Carare. Andresen (1999) found that *A. seniculus* dispersed only 14 species, against 71 species dispersed by *A. paniscus.* This is similar with our findings, and shows the ability of *Ateles* species as a seed disperser, since also relays more in a frugivore diet (as explained before).

Regarding the dispersal distances by *A. hybridus*, we estimated that this species dispersed seeds as far away as 440 m, with the longest dispersal distance of 1 800 m. Link & Di Fiore (2006) for *A. belzebuth* in Ecuador, from 916 collected defecations, registered 28 833 seeds from 133 different species, and only 11 seeds were deposited less than 50 m from the mother tree, four seeds less than

20 m, they also stand that *Ateles* spp can potentially disperse seeds more than 1 250 m away from their sources. The previous reports are consistent with our results, however, their sample size is not comparable with ours, however similar with those authors, our observed tendency for *A. hybridus* to disperse seeds away from the con-specific tree is important.

The seed dispersal ability of *A. hybridus* in the present study, in comparing with the study in Ecaudor with *A. bezebuth,* is important to highlight when considering the differences in the sizes of the study areas. San Juan is an isolated fragment of 66 ha, vs. the 500 ha of Yasuni National Park in Eucador (Link & Di Fiore 2006), which imply that even though the area at San Juan is very small, the monkeys are moving seeds all around the forest, therefore playing a key role as a seed dispersers in the forest.

Habitat use and home range

There was an overlap observed in home rage and habitat use of the three species of monkeys, this can be explained by the fact that this is an isolated fragment where the animals do not have the option to disperse or look for resources in another area. This aspect of the forest studied, together with the high density of each of the monkey species per km^2, could explain our finding that monkeys are experiencing certain changes in their normal patterns of diet and behavior. It is possible that a small fragment influences the normal behavior patterns of the species. Resources and space are likely to be limiting at San Juan and consequently the monkeys are facing feeding stress.

The SJ1 group, with 20 individuals has a home range of approx. 19 Ha; in Ecuador, Link & Di Fiore (2006) found that one group of *A. belzebuth* whit 22 individuals has a home range of 246 Ha. With regard to *A. seniculus* at San Juan, the species had home ranges from 4 to 5 ha. Posada *et al.* (2007) studying the same species in a Colombian Andean Forest, found that five groups that live in a 113 ha. had home ranges between 8 to 14 ha.approximately. Our results showed that both species, *A. hybriuds* and *A. seniculus,* had smaller home ranges than what is reported in the literature, these home ranges are the result of an adaptation to the small fragment they are living on, therefore it is possible to say that both species are being limited by space.

The overlap in habitat use as well as the overuse of the same resources can indicate the occurrence of scramble competition, where animals partition the "limited" resources in the same way. Scramble competition is intensified when groups get larger, if there is not a limit in the group size there will be a threshold below which further reduction in foraging can not be tolerated (Snaith & Chapman 2008). This also implies that at San Juan the monkey species are probably not meeting their nutritional requirements, and this could affect their future survival. In the case of females, the costs of foraging with a low nutritional status is reflected in a reduction in reproductive success, with a direct suppression of the reproductive system. This suppression can be also the result of social stress (Cowlishaw & Dumbar 2000).

Immediately after habitat fragmentation an increase in the population density of large-bodied primates is observed. Isolated populations are able to survive, but with time the competition for resources leads to a population decline. This comes gradually as there is habitat saturation or a "crowding effect", leading to small population size, and extinction. In cases where the populations cannot reach other forests beyond the fragment, and there is an increasing mortality and low ratios between adults and infants, an indicator of declining population (Estrada *et al.* 1999; Cowlishaw & Dunbar 2000; Muñoz *et al* 2008). At this study area and talking only in terms of *A. hybridus* SJ1 group, there are 20 individuals with a ratio 13:5 adults to juveniles. Ramos *at al* (2003), found at two fragmented forest with high degree of disturbance in México for *A. geofroyyi* a ratio of 7:6 (in a 7,7 km^2 area) with a total of 20 individuals and 13:12 (In a 29 km^2 area) with a total of 45 individuals. Comparing these findings with our population ratios adults:juveniles and despite the high density of *A. hybridus* in San Juan, and that new born have been reported, it is possible to say that the population is likely in decline.

Despite the decrease in the percentage time spent on fruit consumption by *A. hybridus* towards the end of the study, its ecological role as a seed dispersed seems to be important. According to Link & Di Fiore (2006), *Ateles* species play an indispensable role as the primary seed dispersers for the maintenance of the tropical forest, and their loss could have implications on the composition and persistence of the tropical forest. In the fragment at San Juan, not only could be affected the fate or viability of the primate community, but also the fate of the forest. We observed an overlap of seeds dispersed by the monkeys, so that they are distributed in areas of higher use. Given they cannot disperse the seeds beyond the relict of forest, with time this could lead to a cluster distribution of the seeds and consequently the number of viable seedlings and number of tree species will be reduced (Schupp 1993). Having in mind the high population densities, the reduced home ranges, and the overlap of the habitat for feeding resources, besides it is a fact that the community of monkeys is adapting and living in this forest relict, there will be a moment when their populations overcome the carrying capacity of the ecosystem, and therefore a regulation of the population size (Begon *et al.* 2008).

Given the current conservation status of *A. hybridus,* it is necessary to avoid this natural process to occur. It is urgent to generate and apply management practices to guarantee the conservation of this species, especially since San Juan de Carare is not an isolated case from the reality many forests are facing in Colombia.

Conclusion

In terms of biodiversity conservation, our findings show the feeding ecology of the primate community is being affected by the habitat fragmentation, this would lead to influence in a negative way the population viability, since it is probable the monkeys are not obtained enough resources for supply properly their daily activities. This is related with the habitat and resources overlap, due to the species can not get resources from another forest.

The sympatric species *A. hybridus, A. seniculus* and *C. albifrons* at the isolated forest fragment in San Juan del Carare, Colombia, are changing their feeding strategies, by shifting their diets (e.g wood consumption or mature leaves), and decreasing their consumption of feeding resources.

The overlap in habitat use and home range is leading to a over-use of the trees and as a consequence there is feeding stress, the species are adapting by showing a higher flexibility of their diet, showing patterns not normally known for the species elsewhere. These changes apply not only to feeding behavior but also to their activity budgets, given the adverse situation they are facing.

The prominent role of *A. hybridus* as seed disperser is remarkable since they are feeding on a wide array of fruiting trees and dispersing many of the seeds, their large big home ranges allows them to disperse seeds long distances and all around the forest.

Estimates of home range and habitat use increases our understanding of the dietary overlap and possible conflict areas experienced by the primate species studied, where the exploitation of the feeding resources can be higher.

Recommendations

Long term studies of these species is necessary in order to get more reliable data about its behavior, ecology and the way their populations are being affected to the anthropogenic impacts. Especially for *A. hybridus,* which is poorly known, given its critical status is necessary to start thinking in proper conservation practices before it be too late, in order to fulfill with the requirement the species needs and guarantee the viability of the remaining populations that are in Colombia. That will be with corridors to link different relicts of forests. Is also important to find the minimum size for forest fragments that can harbor viable populations of *A. hybridus,* as well as to identify species composition-succession stages of forests.

It is necessary to carry out phenological studies in the area, in order to know the patterns of the fruit resources offer along the year (fruit abundances), and better understand the ecological patterns and answers of the species towards the resources availability in this adverse area.

The identification of the flora of the area is very important in order to better understand into what degree plants of the same species are sharing, and have a clearer scenario about the inter-specific competence. Form this also will be possible to recognize the keystone species for them and the forest in order to start the reforestation in at least corridors, to guarantee connectivity with the closest fragments and therefore more extensive habitat for the species.

Is important the long-term study of the monkey community at San Juan de Carare in order to obtain continues data all year round and establish the general patterns of their ecology, in the same way is important to compare with more forest relicts around the area.

It is necessary to generate a reference seed collection and an herbarium, as a reference for all further studies in the area.

Intensify the *ad-libitum* sampling in order to have a more detailed information about the social behavior are important in order two assess more detailed the inter-specific interaction in order to identify in a more detailed way agonistic-encounters between the species.

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Appendix 1 Flow chart of the sampling methods for the study of the primates at San Juan del Carare, Colombia